Pigs and Chips: the Making of a Biotechnology Innovation Ecosystem

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Abstract

This paper presents a longitudinal case study in UK biotechnology covering some 30 years during which genomic technologies were introduced into pig breeding. This case study demonstrates how co-innovation involving existing small and medium sized enterprises, together with contributions from academics, has enabled companies to obtain the resources needed for value creation. Important contributions at critical junctures from public funding, pivotal contributions of individuals, and entry of new enterprises supplying essential resources, have enabled the fruitful realisation of new value creation. This paper contributes to the literature by taking a historical perspective, demonstrating how enabling long-term networking relationships including relevant academics, research institutions, funders and knowledge brokers has the potential to generate an innovation ecosystem that can respond effectively to a range of external challenges and take advantage of new techno-scientific opportunities.

Keywords: innovation ecosystem, animal breeding, biotechnology, Sus scrofa, SME

Introduction

Biotechnological research generates a host of novel tools and knowledge, which, if exploited, could contribute to the bioeconomy. However, a critical step is the translation of these resources into commercialisable products and processes. This paper aims to contribute to an understanding of translation processes through a longitudinal case study illustrating how genomic and biotechnological knowledge was transformed into innovative products in the agricultural sector.

Our research therefore aims to answer the question of how biotechnological innovations have been developed and implemented in practice by the UK pig breeding sector. This paper takes an interdisciplinary approach, combining the strengths of history of science in understanding longer-term developments, with the appreciation of innovation processes provided by science, technology and innovation studies. It also aims to provide new insights into emerging value creation by the processes of co-operation and competition among companies in one industry sector.

The case is that of the adoption of genomics in the United Kingdom (UK) pig breeding industry from the 1980s to 2019. Close examination of this sector reveals it to be far from mundane and traditional. It readily adopts biotechnological and genetic knowledge and methods, and demonstrates the contributions of biotechnology in a wide-range of contexts. In particular, the case study highlights the capturing of value from the 'genomics revolution' that promised so much in the 1990s (Hilgartner, 2017; Watson, 1990), and continues to attract policy and funder interest (Green and Guyer, 2011; Bell and Life Science Strategy Board, 2017). Much of the research undertaken in this area has considered the impact of human genomics (e.g., Glasner and Rothman, 2004; Hilgartner, 2017); less attention has been paid to its impact on livestock agriculture.

The case study is approached from an innovation ecosystems perspective. The innovation ecosystems concept has been adopted both in the business literature and in innovation studies (Gomes et al., 2018). An innovation ecosystem can be considered as "the collaborative arrangements through which firms combine their individual efforts into a coherent, customer-facing solution" (Adner 2006: 2). These collaborative arrangements allow firms to create value in ways that no single firm could undertake alone (Durst and Poutanen, 201: 3). The external environment provides a milieu in which selection pressures act on the ecosystem actors, resulting in new opportunities and threats.

Innovation ecosystems can be contrasted with a linear model of innovation in which development follows research, and commercialisation follows development. We seek to demonstrate that innovation in this case study is more complex and draws on scientific developments, their interactions with market processes, and on research funding policy. External pressures may further arise from biological constraints in our case of pig breeding and production, as well as regulatory environments, although the latter plays only a small role in this case study.

The innovation ecosystems approach allows us to foreground the interactions between different kinds of public and private sector actors, with distinct and shifting institutional drivers and histories. This paper therefore allows us to contribute towards the growing appreciation of the ways in which public and private sector actors are intertwined in research and innovation processes (Didier, 2018; Edgerton, 2012; García-Sancho et al., 2022a; García-Sancho et al., 2022b; Godin and Schauz, 2016; Sunder Rajan, 2006, especially chapter 1; Yi, 2015).

Innovation Ecosystems

A plethora of terminology has been formulated using the concept of the ecosystem to explain aspects of techno-scientific research, development and commercialisation. Examples include: innovation ecosystems, knowledge ecosystems, entrepreneurial ecosystems and business ecosystems (Scaringella and Radziwan, 2018; Xu et al., 2018). Key to innovation ecosystems are networks and social relationships, both formal and informal, embodying trust and tacit knowledge (Scaringella and Raziwan, 2018).

Papaioannou et al. (2009: 319) refer to innovation ecosystems as "a complex network of interdependent relationships". Granstrand and Holgerson (2020:102101) suggest a more focused definition which involves an "evolving set of actors, activities, and artifacts, and the institutions and relations, including complementary and substitute relations, that are important for the innovative performance of an actor or population of actors".

The innovation ecosystem concept takes ideas from biology and applies these to business, a transference that has been critiqued. Oh et al. (2016), for example, argue that innovation ecosystems could equally well be described as innovation systems, and that ecosystems, unlike innovation systems, do not have a clear purpose. In contrast, Shaw and Allen (2018) argue that both natural ecosystems and innovation ecosystems are complex systems producing valuable outputs. Walgrave et al. (2018) identify innovation ecosystems with specific goals, or what they term "ecosystem value propositions". Ritala and Almpanopoulou (2017) distinguish between systems that have been engineered (often by public funding policies) and those that co-evolve (as a result of market drivers). They pinpoint the emphasis on co-evolution as a key aspect of an ecosystem approach. Pushpananthan and Elmquist (2022) emphasise that a combination of competition and co-operation distinguish innovation ecosystems from innovation systems.

For Shaw and Allen (2018), a key motivation for articulating an approach using the ecosystem analogy, is how it enables the comprehension of flows of resources, in particular the re-circulation of resources typical of an ecosystem. Walgrave et al's (2018) "ecosystem model" foregrounds the examination of the structure of the innovation ecosystems and how, as a network, this system creates and delivers value. Furthermore, compared with innovation systems perspectives, the innovation ecosystems approach emphasises collaborative and complementary interactions between distinct actors, and exchanges between sectors rather than focusing primarily on competitive dynamics within a sector (Granstrand and Holgersson, 2020).

We therefore suggest the innovation ecosystem concept provides an appropriate analytical basis for our case study, because our focus is on interrelationships among academics and industry actors (Dedehayir et al., 2018) and the co-evolutionary processes involved in creating value. Our emphasis is on the mechanisms associated with value creation: how enterprises obtain resources to create value for customers, and how technology and ideas interact with each other. Our longitudinal approach focuses on what actors actually did, and on who had power to influence the course of events (Sotarauta and Mustikkamäki, 2015).

By contrast to innovation systems approaches that are often anchored in specific geographical domains, the innovation ecosystem concept is often applied to individual firms and their supply chains. This enables researchers to range more freely across sectoral and geographical boundaries. Here, we consider an industry sector, namely companies supplying breeding pigs to farmers, in its interactions with a different sector, academia.

Method

This research is a longitudinal qualitative case study (Yin, 2003). This historical dimension has enabled us to discern long-term trends and changes across the industry and academic sectors concerned, and the interactions between them.

We interviewed personnel from across the companies and academic institutions involved in pig breeding, as well as knowledge brokers and policy-makers. We collected data during 2018-2019 by 37 semi-structured interviews, and two focus groups consisting of thirteen and four participants respectively. Interviewees and focus group participants were chosen on the basis of their previous or current involvement in some aspect of the pig breeding innovation ecosystem. They were identified in part through one of the author's investigations into the history of pig genetics and genomics, which included network analysis of publications derived from submissions to data repositories, and from the other author's experience of the animal breeding sector and research on agricultural innovation. Additional interviewees were identified through snowballing from suggestions and mentions in interviews themselves. We also undertook extensive searches of scholarly, grey and commercial literature as well as inspecting historical archives (including of the Roslin Institute and personal archives of two respondents). This enabled the information provided in the interviews to be further assessed. Interviews were conducted by the two authors. A sample of interviews were undertaken by both interviewers ensuring consistency of approach. Ethical approval was given by the University of Edinburgh.

Due to the flow of personnel between industry and academia, as well as within industry and academia, it is only possible to broadly indicate a respondent's affiliations. The following interviews were undertaken: ten people from the UK pig breeding industry, four people from UK academia and four policy-makers. Additionally, three people from European pig breeding organisations and sixteen non-UK based academics were interviewed. Data were analysed inductively, paying particular attention to key themes arising from descriptions of interactions among industry and academia. The focus of this case study is the UK, but given the international nature of both the science and the pig breeding industry, reference will be made to developments in other jurisdictions where appropriate.

The longitudinal study starts by considering UK pig breeding in the 1980s, prior to the advent of genomic sequencing and the Human Genome Project. Instead, it was an era dominated by quantitative genetics approaches to breeding. Quantitative genetics is based on physical measurements and statistical inferences as to the underlying genetics, relying heavily on computational methods. We trace the impact of the opportunity that progress in mapping the human genome provided to pig breeders – could they take the steps necessary to create value from these new and potentially disruptive technologies? Next, we examine the evolution of the ecosystem to take advantage of genome mapping and sequencing methodologies and technologies. This required collaboration among the pig breeding companies as well as co-innovation with academics. The entry of new companies that specialised in producing Single Nucleotide Polymorphism (SNP) chips proved a critical milestone. New theoretical developments identified ways of using genomic data and tools in improved ways, making what became known as 'genomic selection' possible, but also challenging existing breeding practices. We then consider perspectives on commercialisation, to complement the focus on technological development. Finally, we review the current state of the innovation ecosystem. The focus throughout this paper lies on the relationship between industry and academia, and the way in which economic value has been created from advances in genomic science.

Findings and discussion

State of the UK pig industry in the 1980s

We begin our examination in the 1980s, prior to the commencement of whole-genome sequencing projects such as the Human Genome Project.

An innovation ecosystem can be considered as consisting of specialist organisations (actors and actants – including non-human ones) interacting with each other and in the context of a common environment (Pigford, 2018). After Walgrave et al. (2018), we consider the system goal as forming the boundary of the ecosystem, so defining the actors, actants, institutions and actions needed to produce this goal. A summary of these is provided in Table 1. The ecosystem that we are examining consists of academic research institutions and pig breeding companies with pig farmers as intended customers. A number of ancillary and brokering organisations exist in the ecosystem, notably the Meat and Livestock Commission (a levy body now part of the Agriculture and Horticulture Development Board) and government research funders. The goal of the system is to apply genomic information to producing breeding pigs for farmers.

Pig breeding companies are key actors in this system. In the 1980s, UK pig breeding was dominated by around ten companies, although individual smaller pedigree pig breeders also existed. Breeding companies maintained strong links with the Edinburgh-based Animal Breeding Research Organisation (ABRO) as well as animal breeding and genetics expertise at the University of Edinburgh. An Edinburgh-based research institute of the Agricultural and Food Research Council (AFRC; Agricultural Research Council up to 1983), ABRO later became part of the Roslin Institute, a key actor in academia-industry relations (García-Sancho, 2015; Myelnikov, 2017). Although a number of universities also had genetic expertise (e.g., Wye College University of London and Leeds University) their role in the ecosystem of pig breeding is less clear. Roslin Institute and its predecessors were set up to provide strategic research to industry (Button, 2018; García-Sancho, 2015), so unlike universities, they have a history of strong interaction with industry, which in the pig context dated back to the 1960s. For example, the lead product of the company PIC was named 'Camborough' to acknowledge the veterinary expertise from Cambridge University and genetics expertise from Edinburgh University involved in the development of the company.

The links between the research and commercial sector were close. In the words of John Webb, who worked at ABRO and later with a pig breeding company (interview data), "everything was aimed at making the industry successful". Multiple interviewees indicated that links were developed through companies actively going to the institution for advice, through consultancies and through an active recruitment of staff from the animal breeding MSc run by the University of Edinburgh. After the 1980s, the pig breeding

Table 1. Summary of actors, activities and artifacts in the innovation ecosystem

Actors	Activities	Artifacts/products
Pig breeding companies (e.g. PIC)	Using genetic and genomic technologies	Breeding pigs supplied to farmers
Publicly-funded research institutes (e.g. Roslin Institute)	Basic and strategic research	Statistical procedures, software programmes, genetic and genomic data and knowledge (including theory)
Universities (e.g. The University of Edinburgh)	Basic academic research	Statistical procedures, genetic and genomic data and knowledge (including theory)
DNA sequencing centres (e.g. Sanger Institute)	Large-scale, high-throughput DNA sequencing	DNA sequence data
Meat and Livestock Commission (a levy board)	Comparative data on different pig breeds; expertise on artificial insemination	Pre-competitive innovation for the breeding sector; information on value of products of breeding sector for producers
Pig Breeders' Roundtable/UK Pig Breeders' Consortium/Pig QTL consortium	Collaboration among pig breeding companies	Cross-sectoral understanding to smooth translation
Farm Animal Industrial Platform; European Forum of Farm Animal Breeders	Advocates for pig breeding at European level	Conduit to European-level policy-makers
European Commission	Research funders	PiGMaP, successive research projects and enduring collaborative relationships
Agricultural and Food Research Council; Biotechnology and Biological Sciences Research Council; Ministry of Agriculture, Fisheries and Food; Department for Environment, Food and Rural Affairs	UK research funders	Genome mapping, support for publicly-funded research institutions
Meishan pigs	Crossing with European breeds	Reference families containing many differences at the genomic level (polymorphisms) to enable genome mapping
Canadian research group	Research group identifying causal mutation for porcine stress syndrome	Enabled development of genetic test to detect the mutant gene
Genesis Faraday Partnership/Biosciences Knowledge Transfer Network	Knowledge brokers	Relationships between sectors, new translational research programmes
Illumina	Developed standard platform for genomic analysis	Pig SNP chip, DNA sequencing services

companies were also able to collaborate on training PhD students and hosting post-doctoral students. Consultancies were in place from the 1960s. One interviewee explained how consultancies produced questions which the academics then sought to answer (e.g. appropriate replacement rates for breeding stock), as well as translating information from academia to industry. The pig breeding sector was typified by strong links between academics and a highly-trained industry sector. Several of our interviewees emphasised the informal nature of contacts between industry and academia and the ease of communication between the two. Staff from the pig breeding companies attended academic conferences such as World Congress on Genetics Applied to

Livestock Production, the International Society for Animal Genetics and to a lesser extent the European Federation of Animal Science (formerly European Association for Animal Production). From these conferences, staff in pig breeding companies were able to follow-up lines of work that they assessed as promising for potential translation to the breeding sector, on an informal basis with the individual researchers. Through these interactions, scientific interests were able to overlap with industry interests. Furthermore, as John Webb (interview data) argued, the "small size of pig breeding industry in 1970s and 80s ensured totally fluid dialogue between industry and people doing the research", as did the dominance of Edinburgh University allied with ABRO and later the Roslin Institute as the main source of information on genetics research. According to animal scientist and innovation broker Chris Warkup (interview data),

> It wasn't just push from Roslin, it was also because of the history that was clear … industry knew where the expertise was and you didn't have to go shopping for it, it was all in one place.

This advice was particularly important for smaller breeding companies that did not possess the ability to undertake research themselves.

The pig breeding companies in the UK competed against each other for market share. The then Meat and Livestock Commission ran trials from 1984 to 2007 at a central facility, the UK pig industries Development Unit at Stotfold in Bedfordshire, to compare pigs from different breeding companies in a common environment and make these data publicly available to pig farmers. It was suggested to us by an interviewee who had worked in this arena that these external comparative data provided an incentive for the breeding companies to invest in genetic gains, as the availability of such performance data would mean that marketing could only sell genuine improvements rather than mask underperformance.

Although competing to sell to pig farmers, the companies had a common purpose in using genetics to improve the economic value of their breeding animals. Many of the companies supplied breeding pigs to global markets with an emphasis on lean meat production. To this end, the companies were able to collaborate at a pre-competitive level. Examples of this include the Pig Breeders' Roundtable and the UK Pig Breeders' Consortium.

The Pig Breeders' Roundtable was initiated by John King from ABRO. It was modelled on a similar, successful initiative in the poultry industry that brought together industry and researchers in a closed event, without papers being published. Multiple interviewees told us that this was a very successful model of interaction, with corporate staff willing to speak about their breeding programmes. Pig breeding companies were scattered around the UK. At the outset of the 1990s they were, nevertheless, organised into a British Pig Breeding Companies Committee, chaired by Rex Walters of the breeding company Masterbreeders. This and its later instantiation as the UK Pig Breeders Consortium provided support to academic research on pig genome mapping, as we discuss below.[1]

Regulation of breeding practice has played a relatively modest role in this breeding ecosystem.[2] The purpose of regulation has been primarily to ensure the quality of breeding pigs being sold, the main example being EC Directive 88/661/EEC on the zootechnical standards applicable to breeding animals of the porcine species. This Directive specifies the need for recording pedigrees in order to harmonise herd-books and registers for intra-community trade in breeding pigs. Animal welfare and environmental regulation has additionally been important, particularly for production aspects.

Other jurisdictions apart from the UK have similar strong links between academia and industry, notably Wageningen University and pig breeding organisations in the Netherlands. Land grant universities such as Iowa State University in the United States receive funds from the United States Department of Agriculture's Agricultural Research Service as well as the National Institute of Food and Agriculture (NIFA; the Cooperative State Research, Education, and Extension Service up to 2009). This funding, like the USDAs intramural funding of its own research institutes, is predicated on conducting research oriented towards, and often in collaboration with, breeding and producer industries. Part of NIFA's remit is 'cooperative extension', in which departments of land grant universities work directly with producers to adapt and implement scientific research in the field.

In 1988 the UK government unexpectedly shifted UK research funding away from so-called 'near-market research', imperilling the kind of strategic research of value to industry characteristic of many agricultural institutes (Read, 1989). This was a culmination of a process from the early 1980s that in the opinion of John Webb (interview data), "meant that [industry] became a dirty word". This change in the UK funding environment displaced attention towards the increasing levels of funding available from the European Commission (EC).

EC genome sequencing projects and industry collaboration

Starting from what the industry perceived as a competitive advantage in livestock breeding in Europe, at the turn of the millennium the Farm Animal Industry Platform (FAIP; see below) argued for continued investment by the EC in genomics research to maintain that competitiveness against USA, Japan and China, as well as private companies such as Monsanto who had recently entered the pig breeding business. FAIP posited that no one single company had sufficient funds, facilities or knowledge to undertake the work on their own (FAIP, 2000). Indeed, in developing their technical genetics expertise, the challenge for pig breeding companies was that this science was expensive but the margins from pig sales were low. Therefore, profits were too low to allow individual pig breeding companies to invest in developing capabilities in this area.

Although the companies competed, collaborative work was therefore necessary to begin to realise the benefits of the 'genomics revolution'. As Chris Warkup notes, moving from quantitative genetics to using molecular genetic information required a paradigm shift from the companies (interview data),

> These businesses didn't have big R&D Departments that could talk to each other about how they should handle this, they didn't have big consultancy budgets, they worked their way through it by actually having conversations with their competitors, how are we going to do this?

The first porcine genome mapping initiative funded by the EC was PiGMaP (1991-1996). The aim of PiGMaP was to populate maps of pig chromosomes with various kinds of genetic markers, and to develop molecular, statistical and informatics tools to be able to more densely populate these maps and then to identify areas of the genome associated with variation in measurable traits (Lowe, 2018). Chris Warkup (interview data) suggested that for breeding companies, joining in with PiGMaP was "the cost of staying in business … You will go out of business if you do not invest in the latest technology".

Hervé Bazin, a scientific staff member in the EC's directorate-general XII for research (DG-XII), was instrumental in guiding and advising the nascent PiGMaP collaborators in the development and approval of their project, indicating additional opportunities beyond PiGMaP to develop the work still further. He encouraged leading academic drivers of PiGMaP such as the Roslin Institute's Alan Archibald and Chris Haley to seek out industry support as well as academic collaborators. Industry support played a role in securing funding from the project from the EC. Furthermore, an initiative driven by breeding companies and Roslin Institute resulted in the importation of a small population of Chinese pigs of the Meishan sub-breed into the UK in 1989. These pigs were critical to the reference populations at the heart of PiGMaP, along with separately established populations of Meishan pigs in France and the Netherlands, and wild boar populations in Sweden and Germany. Just as no single institution could obtain sufficient national funding to map the pig genome, no one institution could perform the different kinds of mapping and analysis required, so tasks were divided and coordinated across 21 institutions (most, but not all, in Europe).

The outputs of PiGMaP and succeeding EC-funded projects represented the creation of platform technologies (e.g. Kim and Kogut, 1996) accessible by pig breeding companies. This built on existing practices of free sharing of statistical software applications for animal breeding and genetics (Rothschild et al., 2003). The way in which the genetic information from PiGMaP was used to create market value remained, however, in the control of individual organisations.

Across academia, industry and DG-XII, several individuals helped to adapt livestock genetics research to the changing funding and policy environment. Old niches had to be abandoned, and new ones constructed and occupied, which entailed forging both deeper collaborative relationships across sectors and borders, as well as reorienting institutions to make them more responsive to collaborative opportunities whenever they might arise.

Early in the formation of PiGMaP, Roslin Institute director (1988 to 2002) Grahame Bulfield attempted to secure funds to create an academic 'Network for Farm Animal Genetics', which failed. In its stead, on Bazin's advice, to foster further post-PiGMaP projects and to establish a body with which dialogue with EC bodies could be initiated, the Farm Animal Industry Platform (FAIP) was inaugurated in 1995, with considerable impetus from Graham Plastow of the company PIC, Gerard Albers of Nutreco and Jan Merks of Topigs (who initially led FAIP). Informal brokers such as Bazin were central to this innovation ecosystem. Furthermore, this developing set of relationships depended on leadership from multiple people (as per Dedehair et al., 2018; Sotarauta and Mustikkamäki, 2015).

Knowledge intermediaries have been identified as key actors in innovation systems (Klerkx and Leeuwis, 2008; Klerkx and Aarts, 2013). The founding of the Genesis Faraday partnership in 2003 as a knowledge intermediary organisation, was another key governmental intervention. It was one of 24 Faraday Partnerships introduced by the then UK Department of Trade and Industry, driven in particular by Science Minister Lord Sainsbury to improve the commercialisation of UK research. The initiative was described by Chris Warkup, the CEO, as providing a "centre of gravity", a link with government and a source of encouragement for a livestock industry that at the time felt beleaguered as agriculture – and livestock agriculture in particular – had faced declining research funding and political importance with the merging of the AFRC into the Biotechnology and Biological Sciences Research Council in 1994, and the Ministry of Agriculture, Fisheries and Food into the Department for Environment, Food and Rural Affairs in 2001.

From single-gene hunting to marker-assisted selection

The mapping of the pig genome held the promise of ever more fine-grained resources and tools for the localisation of genes and mutations that may be implicated in particular traits of interest to the industry. This promise was considerably fuelled by research that led to the discovery of the Halothane gene which led to quickly-implementable tests and economic gains in the industry.

In the 1970s, the pig industry had started to struggle with poor quality meat and the sudden death of pigs when stressed (porcine stress syndrome). Inadvertently, selection for pigs with large hams led to selection of a linked mutated gene that caused both poor meat quality, and a predisposition to sudden death. Termed the halothane gene, because an early test for presence of the mutation was to administer halothane anaesthetic to the pig and to observe any resulting rigidity in muscles, the gene causing this effect was identified by a Canadian group in 1991 (Fuji et al., 1991). The discovery of the halothane gene enabled pig breeders to identify pigs which carried the mutation and use genetic tests to remove them from their populations. In the view of many of our interviewees, this provided a real, commercial advantage to using genetic information on a single gene.

The identification of a single gene raised the question of patents. The relevant gene (*ryr1*) was patented by academic and hospital-related organisations (the gene variant is also present in human populations), but individual breeding companies were unable to obtain exclusive licenses for testing for the gene variant. The result (according to multiple interviewees) was that tests for the gene were quickly and widely adopted across the pig breeding industry, giving the sector a large economic and animal welfare advantage.

In the 1990s, according to one of our industry interviewees, some companies felt that patent protection would enable collaborating researchers to publish their research and thus create a win-win scenario, where both parties were satisfied and could continue to collaborate. Peer-reviewed publications were also seen to be important by industry, not only to maintain collaborative relationships with academics, but also in order to establish credibility for both marketing and further staff recruitment.[3] Patented pig genes include HAL 1843™ (halothane gene), *ESR* gene polymorphisms to improve litter size and the *KIT* gene. Breeding companies also used copyright protection e.g. PIC held rights on Berkshire Gold™ for pigs that were 100% Berkshire breed in origin, and PICmarq™ to indicate that gene marker information was used in the selection of these pigs (Rothschild et al., 2003). The high prevalence of PIC named in patents in part reflects PIC's (and its later identity as Sygen) listing on the stock exchange where the number of patents held was one of the metrics communicated to investors.

Our interviewees from different breeding companies suggest that the trend towards patenting did disrupt the innovation ecosystem, particularly when Monsanto entered the pig breeding sector in the USA when it took over DeKalb Genetics in 1998, and started to patent not just genes but also breeding practices.[4] The European industry reacted by setting up a 'patenting watch' through the European Forum of Farm Animal Breeders (EFFAB; this superseded FAIP in 2004) to ensure that they were aware of developments. In the event, breeding companies found patents too cumbersome to maintain and resorted to trade secrets instead (focus group data), and Monsanto withdrew from the pig breeding sector. Multiple interviewees identified patenting as not significant in their current practices. The patenting that could have created a strong selection pressure and positive feedback loop advantaging particular companies proved not to be a mechanism that worked well in the context of the pig breeding industry. The private holding of data concerning the pedigrees and performance data on the pigs in their possession, and the holding of those pigs themselves in biosecure nucleus herds are other long-standard and significant proprietary practices in the industry.

The halothane gene mutation stimulated commercial interest in single genes. As a focus group respondent related, "people began to think what else could be segregating that would be amenable to using genomics." In the event, apart from the halothane gene, single gene effects were mostly restricted to genes of local national interest such as *RN-* gene concerning meat quality of French Hampshire pigs.

As single genes of large-effect proved difficult to identify, the industry (and academic researchers) resorted to attempting to identify genetic markers that were associated with traits of interest. There was initially a great deal of enthusiasm for adopting what was termed Marker Assisted Selection (MAS). However, moving from the PiGMaP resource populations to using genetic tools in commercial populations proved not to be as straightforward as first envisaged due to differences between the mapped populations and the breeding company herds, and the still sparse maps meant that markers could be distant from causative genes.

MAS later proved not to be helpful as originally hoped, as relationships between markers and genes broke down over generations. Additionally, it proved too difficult and costly to identify markers closely linked to individual genes, most of which had but small effects on the production traits of interest anyway. In this period, one former industry scientist retrospectively reflected that "the power of genomics was overestimated except for its marketing impact; we were victims of the success of the halothane gene".

Although PiGMaP produced little implementable results directly, it and other contemporary mapping projects were essential for subsequent developments. The entry of new companies to the innovation ecosystem, and the development of SNP chips, constituted another crucial stage in the development of the innovation ecosystem.

Introduction of SNP chip companies to the ecosystem

Single Nucleotide Polymorphism chips (SNP chips) are slides with specific DNA sequences attached to them. They are used to detect the presence or absence of complementary strands of DNA in samples run through them, therefore *genotyping* the source of the sample for the set of markers (SNPs) contained on the chip. In livestock, the first commercial SNP chip was produced at the instigation of the USDA for cattle in 2007, by Illumina. It contained 54,001 SNPs, and was used in genomic evaluations of American dairy cattle.

The value of such a chip for pigs was apparent to academic researchers. Representatives from Illumina and another chip manufacturer, Affymetrix, presented their case to the researchers at the Plant and Animal Genome conference in January 2008. Illumina won out, in part because of the lessons they had learned with the cattle chip. The eventual product of this collaboration between established pig genome researchers and a company that had only just entered this particular innovation ecosystem from an entirely different industry, was the 62,121 marker 'PorcineSNP60' (Ramos et al., 2009).

This marked a move towards evaluating breeding value of individual pigs on the basis of both physical and genomic data. Its advent was enabled by, and made use of, the masses of sequence data arising from projects to sequence the whole genome of the pig, producing a 'reference genome'. In this respect, it represents the creation of a technological platform and standard that itself derives from the platforms and standards established in genomics.

The creation of standards and platforms have been a central feature of the development of genomic infrastructures (Hilgartner et al., 2017; Strasser, 2019). The platforms include genome mapping and DNA sequence databases (Maxson Jones et al., 2018). The standards include the ways in which data and metadata are recorded in databases, the norms of submission and release of data, and ways of representing data (Hilgartner et al., 2017; Maxson Jones et al., 2018; Stevens, 2018). For example, the annotated reference genome for the pig (itself a standard), is represented for use by researchers on a platform (the Ensembl genome browser), which itself incorporates multiple standards and makes use of the data held by databases. The infrastructure of genomics represents a kind of platform ecosystem, "a system or architecture that supports a collection of complementary assets" (Thomas et al., 2014: 200). One of those complementary assets that it supports is the formulation and production of a SNP chip. A SNP chip is also a technological platform, and manifests as a standard, if accepted and widely distributed. This was the case for PorcineSNP60, due to the upstream involvement of multiple members of the pig genomic research community and industrial actors.

The technological artifact of the SNP chip was essential in being able to identify a large number of genetic variants simultaneously, rather than relying on testing for individual genes or markers, or mere dozens thereof. In the view of our interviewees, even though the first reference sequence was far from perfect, and was missing portions of the genome, the first 60k chip was extremely useful for industry. One of our focus groups noted that SNP chips made their work a lot easier, as one interviewee commented: "just squirt on (effectively) the DNA and suddenly you get the genotypes".

At the same time, theoretical developments from academia provided a basis on which this information could be used for pig breeding. This involved combining the information from thousands of SNPs to evaluate the breeding value of a pig, without knowing the functional implications of the individual SNPs. One industry interviewee described how a seminal theoretical paper by Meuwissen, Hayes and Goddard (2001) was originally treated with scepticism, and the theory of 'genomic selection' took a while for industry to accept. But once accepted, it became a valuable next step for the industry in using genetic information to complement physical measurements.

The first published data analysis from SNP chips came from academia (Ramos et al., 2009). What happened next is described by a focus group member:

> First there was the map, then eventually the SNP chip and then everything just took off. The SNP chip took off because we had the initial sequence in 2008 and that led to the SNP discovery that led to the chip and then things took off.

The use of SNP chips has had a significant effect on the structure of the pig breeding industry. The predictive models of genomic selection are more accurate when the reference populations used to generate them are larger. Access to more animals, more data on their performance and pedigree, and ability to invest in expensive genomic technologies, provide a competitive advantage. Consequently, breeding programmes became more expensive to run and therefore accelerated industry consolidation.

SNP chips have been adopted in the pig breeding industry on a short time-scale, especially compared with biomedical innovations. As described by one of the focus group members:

> The distance between research and application is extremely short in comparison to what you have to do to prove a drug works or whatever. It takes years of validation, you also have regulatory oversight from governments…In this [pig breeding industry] case we're working directly with industry, once industry knew that it was working and they could adopt it, boom, they took it and they would run with it faster than what the researchers probably could keep up with.

Table 2 provides a summary of the interactions within this innovation ecosystem, following environmental challenges. It shows a simplified schematic of flows of knowledge (indicated by arrows) concerning the use of genomic information to create value.

As well as the theoretical development, modelling, statistical methods and matrix algebra required to establish selection using SNP chip information, other developments were also important for enabling this innovation, including increases in computing power. There were also biological requirements such as pedigree structures appropriate to enabling the adoption of genomic selection. This, in turn, benefitted from the development of artificial insemination, which the Meat and Livestock Commission had an important role in developing, providing yet another link between industry and research.

Although genomic technologies were rapidly adopted by industry, the industry view was that pig farmers would not pay any extra for the harnessing of these advances. However, in order to remain competitive, genomic technologies were needed. This market pull, if indirect, had a real impact on the relative market share of different pig breeding companies.

Link between scientific possibilities and commercial realities

Internal company processes, and in particular the role of key individuals (both in academia and industry) has had a strong influence on innovation trajectories. Choices made by technical directors and chief executives did affect the direction of travel of different companies.

Instituting a genetic selection programme does not usually visibly affect the resulting pig. Furthermore, genetic changes tend to be gradual and not easily perceived in the short-term, although because they are cumulative, over the longer-term changes can be substantial. Our interviewees emphasised how trust in the person advocating the technical process was key to genetic programmes being accepted. As one of the focus group members put it (their emphasis): "somebody has to <u>believe</u> genomics is going to help the world". This trust was also described as a cumulative process, and while economic arguments were often needed, the key was trust in the person making the proposal.

Individual company history can also have a big influence on the direction of innovation. A clear example of this is the relationship between the pig breeding company PIC and Dalgety plc. Originally an initiative of four Oxfordshire pig farmers in 1962, PIC needed extra investment to continue to grow and was bought out by Dalgety in 1970. Dalgety had a range of different agricultural interests which included a biotechnology lab loosely associated with Cambridge University. This established a link between PIC's pig breeding expertise and the molecular methods deployed in biotechnology. This relationship influenced PIC to become involved in molecular genetics, and was instrumental in PIC looking to apply biotechnologies to the pig business in ways that other companies were not. PIC, under its new owners Genus, have continued this focus on biotechnology and have publicly announced that they have entered the era of genome editing, intending to introduce genome-edited disease resistant pigs to China (Genus, 2021; Whitworth et al., 2016, Burkard et al., 2017).

Not all the companies that expected benefits from genomics continued to be successful. The giant of genetically modified crops, Monsanto,

Table 2. Summary of interactions within the innovation ecosystem

Timeline	Outputs	Academics	Industry	Environmental change
1980s	Advice on breeding programmes			
1988				Public funding of near-market research axed
1989				Introduction of Meishan breed to UK
1990-2003				Human Genome Project
				EC Funding
1991-1994	PiGMaP resources			
1991		Halothane gene identified		
1995				Farm Animal Industry Platform established
1997-2013	Projects to identify Quantitative Trait Loci linked to phenotypic variation and enable MAS			EC funding
2001		Seminal academic paper on use of multiple SNPs		
2003				Genesis Faraday Partnership established
2007				SNP chips developed
	Genomic selection undertaken			

also entered the global pig breeding frame after it bought the US company DeKalb Genetics in 1998, which included a pig breeding arm. However, after a short time, Monsanto withdrew from the pig breeding business. The well-known human biotechnology firm, Celera, also developed an agricultural arm, Celera AgGen, which was subsequently sold to private company MetaMorphix. The company offered a 'Whole Genome System™' to test for genetics of production traits. MetaMorphix subsequently went bankrupt. It seems that being a large company, with expertise in genetics and genomics in other species, is not sufficient to successfully compete in the pig breeding ecosystem.

Having the genetics and genomics expertise is only one part of the package needed to compete in the ecosystem. This knowledge needs to be implemented and allied to a distribution network and appropriate business model. Samples have to be taken from the pigs and then stored, animals have to be identified, and data have to be processed. Van der Steen et al. (2005) describe some of the processes adopted by PIC. One of our industry interviewees indicated that sometimes appropriate compromises have to be made from 'book practice' to practical application, and knowing which compromises can be made is part of the craft of pig breeding.

Current status of the innovation ecosystem

There has been considerable consolidation among the pig breeding companies in the UK, with three major companies remaining: PIC, JSR-Topigs Norsvin and Rattlerow. A number of smaller independent breeders also continue to exist. Consolidation has been allied to a drop in the number of UK pig producers, attributed to competition from lower cost countries such as Thailand and Brazil, regulatory constraints related to animal welfare, feed regulations to limit diseases, and also as a result of disease outbreaks, notably Foot and Mouth Disease. Pig production chains have become integrated with meat processors with the result that interactions with individual farmers have been in part replaced by interactions with large integrators, who are internally able to compare the performance of pigs from different breeding companies. Pig production in the UK has been through periods of poor profitability and is very cost-conscious.

The relationship between academia and industry has also changed, though interviewees varied in their evaluation of the extent of the changes that have taken place. The research side has become very data hungry, with demands for pedigree records and physical measurements (the phenotypes) on 10,000-30,000 animals in order to undertake genomic research. It is unrealistic for publicly-funded research organisations to keep such large numbers of animals and therefore researchers rely on collaboration with industry in order to gain access to these animals. As one of our academic interviewees pointed out:

> Once the genomic tools were available the valuable entities were the phenotypes, so the companies have the phenotypes, why should they give those up to other people.

A second change has been the increase in speed at which novel developments are adopted. People in industry are hungry to keep at the forefront of breeding research and have adopted an ad-hoc, opportunistic approach. Alan Archibald, one of the key people involved in getting together the PiGMaP consortium, suggested that the era of the research consortium has passed because the gap between doing the experiment, getting the results and implementation is so short, so it is no longer pre-competitive research. Personal links, however, remain important. Industry personnel network by attending conferences and use personal contacts to become aware of academic research before publication. Bigger companies are able to maintain these interactions, but smaller companies that need it most may not have the resources to do so. Ideas from industry to research groups are also spread through these informal interactions; industry technical staff know the academics who are publishing and are able to keep up to date.

From our interviews, it is apparent that the relationship between academics and industry has changed. What is less clear is the nature of the change, as there is disagreement in the descriptions of our respondents. This suggests that there is more heterogeneity in the relationships than in the past.

It seems that much research has transferred from the public sector to the private sector. However, industry respondents that indicated they also felt academics have become more secretive because of a heightened need to publish due to the increased competitiveness of grant applications, the ever-rising importance of academic metrics and, in the UK, the Research Excellence Framework and associated impact agenda. An alternative viewpoint felt academics have become more reluctant to share their work because research institutions have become more competitive, developing spin-off companies that companies had to buy into in order to get a share of the research. Others thought that it started to become difficult for industry to work with academia when chip technology became available. There was also a suggestion that the nature of relationships between industry and academia have changed from the personal to the transactional. Others disagree. One academic interviewee argued that the "whole community is a translational community".

The future of the pig industry looks challenging, with social concern about pig production methods, challenges to the abattoir sector from shortage of workers, inflationary pressures particularly on feed and energy costs following war in Ukraine, the imperative to maintain pig health with minimal recourse to antibiotics and, in the UK context, changes in trading relationships due to Brexit. It remains to be seen whether continued advances in biotechnology can enable pig breeders to aid producers to maintain resilience in the face of such challenges.

Conclusions

This case study describes some of the dynamics of competition and collaboration among pig breeding companies in the UK, as they have sought to capture the benefits of the genomics revolution. It demonstrates both the complementary and substitutionary effects of innovation (Granstrand and Holgersson, 2020). Innovation based on genomics both complemented existing approaches to pig breeding based on quantitative genetics (for example, concerning the structure of breeding herds and measurement practices), and inaugurated genomic selection, which has the potential to displace many existing breeding approaches and practices. Supplementing Papaioannou et al. (2009), we provide an example of a case where innovation was far less driven by a social history of division of labour and market forces, and far more by a social history of interaction and collaboration. Much of the subsequent innovation was driven by necessity, the low margins and high cost of research, by the limitations of biology (many genes have such small effects to make identifying them barely worth the time and expense) and by individuals who drove the processes of collaboration and convinced their company leaderships to invest in a product for which the benefits would not be apparent in the short-term.

Unlike some hub ecosystems (e.g., Nambisan and Baron, 2013) innovation was not driven by a single firm acting as the leader. However, individuals in academia, such as Alan Archibald, Chris Haley and Max Rothschild, individuals in industry such as Graham Plastow, and numerous others, have had critical roles in this innovation ecosystem at various times. In large part, this has been due to their combined focus on the possibilities arising from cutting-edge science and their appreciation of the practicalities of applying this science. Archibald and Haley were able to influence the course of events by bringing together groups of actors, using what Sotarauta and Mustikkamäki (2015) call "network power". These were not individuals *given* a role within an organisation, but rather individuals who took it upon themselves to stimulate interaction.[5] Of course, successful interaction would have been impossible without the positive contributions from many others. Innovative people inside the breeding companies were embedded in social networks outside the companies (Bagchi-Sen et al., 2011) enabling them to co-create knowledge that was immediately transferable to the commercial setting. It is also clear that one individual, Hervé Bazin, was critically important in facilitating (European) public funding at a crucial stage.

The social networks in this innovation ecosystem are not geographically bound, but depend on a history of interactions that spans decades, and in turn extends to global markets. Sharing knowledge and co-innovation (Dedehyir et al., 2018) in this case study has not depended on co-location, but on a shared focus on a product and ability to leverage the 'genomics revolution'. Using the terminology of Russel and Smorodinskaya (2018), interactions among SMEs and academics took place at a number of different levels from networks, through co-operation to formal collaboration, and back again to networking and co-operation, at varying times during the period of our case study. These links were iterative and did not move only towards closer collaboration.

The case study traces how ecosystem entrepreneurs have created and obtained important resources, such as maps and DNA sequences of the pig genome, together with the infrastructures, expertise and knowledge of biological processes necessary to create value from new scientific developments. It further demonstrates how this was only possible by individual companies working together, even though individual companies have taken different pathways to capture this value. The entry of new ecosystem actors, namely companies providing SNP chips, has been critical to this process. The co-evolution of SNP chips and new statistical methods have provided a selection pressure in the ecosystem. The willingness of executives to invest in these technologies and the availability of research funding at critical moments have proved essential. This ecosystem was not driven by market demand. Pig farmers were not necessarily even willing to pay for genomic selection, let alone demanded the approach. Rather it was driven by a scientific possibility that was recognised by companies, who worked together because they were also competitors and feared losing out if they did not collaborate. In contrast to the crop breeding industry where SMEs feared being taken over by Monsanto (Bagchi-Sen et al., 2011), pig breeding companies were able to maintain their competitiveness, and indeed, Monsanto itself failed to compete.

The ecosystem has benefitted from being a small industry, where people know each other, and the presence of highly technically skilled staff in industry has enabled continued close collaboration between academia and industry. There exists a porous boundary between academia and industry, a long history of collaboration with established research organisations and a culture of sharing, including in sector-specific closed meetings. This has also benefitted from actions of knowledge transfer organisations, such as the Meat and Livestock Commission, the Genesis Faraday Partnership and collaborative organisations at the European level, enabling collective action in support of the industry.

As a single case study, general conclusions have to be drawn with care. However, the case study suggests that enabling long-term networking relationships including relevant academics, funders and knowledge brokers has the potential to engender an innovation ecosystem that can respond effectively to a range of environmental challenges. Its further suggests that these relationships are fluid, and change as the ecosystem itself responds to change. Of course, such long-term relationships could stagnate and fail to respond to environmental challenges, which may result in the collapse of the whole sector.

In conclusion, this case study demonstrates how economic value has been created from basic scientific research and the interactions among scientific developments and individual commitments that were instrumental in bringing this about. In particular, given the gradual and long-term nature of genetic change in a breeding programme, the key role that trust has played in these processes cannot be underestimated.

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Notes

1 As of October 1990, the membership of the British Pig Breeding Companies Committee was as follows: ACS, Cotswold Pig Development Company, JSR, Masterbreeders (Livestock Development), Meteor Pigs, National Pig Development, Newsham Hybrids, Peninsular Pigs, Pig Improvement Company, Pig Link, Premier Pigs, Rattlerow Farms and UPB Porcofram; all but the latter (a plc) were limited companies. Source: letter from Rex Walters to Alan Archibald, 10th October 1990; in 'FP3 BIOTECH' partition, Alan Archibald's personal papers.

2 This does not, of course, apply to the substantial regulations concerning the treatment and welfare of animals under the care of breeding companies, merely that the breeding process itself it not subject to significant regulation.

3 Though company authors do not seem to have been quantitatively important in pig genomics publishing compared with the community as a whole.

4 This takeover, which begun in 1996 with the purchase of a minority stake, was more concerned with DeKalb's work in breeding and selling seed corn. Upon the takeover, Monsanto realised the potential of the hybrid swine breeding section of the company and sought to develop it.

5 One example would be the key role of Grahame Bulfield, Roslin Institute director from 1988 to 2002, in fostering genomic research and links between multiple actors concerned with farm animal genomics, including those in industry, from the late 1980s.