Quantifying Exaptation in Scientific Evolution



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1 Introduction

The rediscovery of a new function for a given object or concept can be just as important as its discovery. This phenomenon is known as *exaptation*, and the related verb is *to co-opt*. It characterises the process of acquiring new functions for which a trait, which originally evolved to solve one problem, is co-opted to solve a new

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problem Gould and Vrba (1982). The definition is similar to the concept of *preadaptation* Bock (1959). However, since this term may suggest teleology, Vrba and Gould urged scholars to replace that term by exaptation. The idea of exaptation was also proposed to distinguish the concept from *adaptation* Darwin (2004). While exaptations are traits that have applications that deviate from their original purpose Gould and Vrba (1982), Kauffman (2000), adaptations have been shaped by natural selection for their current use Bock (1959), Darwin (2004). One canonical example of exaptation in biology is the evolution of feathers. It is often argued that feathers were not originally developed for flight, but emerged in the reptilian ancestors of today's birds for thermal regulation Gould and Vrba (1982). Other examples include the ability of a metabolic reaction network to survive on different food sources which can allow adoption of alternative substrates Barve and Wagner (2013). Exaptation events seem to be important to give birth to adaptive innovations, diversity and, more generally, to complex traits Barve and Wagner (2013).

Gould and Vrba propose exaptations have adaptive and non-adaptive origins: preaptation and nonaptation. Preaptation refers to characteristics or traits that are adapted and 'selected' for one evolutionary purpose (adaptations). These are later coopted to serve another purpose leading to an increase in the fitness of the co-opted trait. Thus, preaptations are adaptations that have undergone a significant change in function Gould and Vrba (1982), Lloyd and Gould (2017). Another source of exaptation is nonaptation. Nonaptation refers to traits that emerge through a process of trial and error that generates lots of 'leftover' features (e.g., DNA, molecules, cells) Gould and Vrba (1982). These concern the effective use of co-opted leftover traits to serve a particular function, but whose origin cannot be ascribed to the process of 'natural selection' Gould and Vrba (1982). Nonaptations are byproducts of the evolution of some other trait Darwin (2004) that do not add to the fitness of the coopted trait Lloyd and Gould (2017), Gould and Vrba (1982). In summary, adaptations, preaptations, and nonaptations are essential processes that drive the evolution of living matter, cells, humans, organisms, and biological ecosystems. They allow us to understand the adaptive and non-adaptive origins of biological novelty.

Recently, the notion of exaptation has been applied to the study of technological change Bonifati (2010), Dew et al. (2004). One set of studies have focused on the development of technological speciation narratives Dew et al. (2004), Levinthal (1998), Andriani and Cohen (2013) and niche construction theory Dew and Sarasvathy (2016). Other studies focused on the adoption of technology Rogers (2010), its commercial application Schumpeter (1939), and its economic impact Dew and Sarasvathy (2016), but not on the origin of those inventions Fleming and Sorenson (2004). Small-scale studies of technological exaptation abound in the management and innovation literature (e.g., Yong Tan and Tatsumura. (2015), Dew and Sarasvathy (2016), Cattani (2005), Rosenman (1988)). These studies point to the role of chance such as serendipitous discovery of a new function Andriani and Cohen (2013). Serendipity (accidental circumstances leading to fortunate findings) and exaptation (a shift in the function of something) are intricately related by the fact that accidental discoveries that contribute to the redeployment of a component in a different context lead to a shift in the function of that component. A related stream of research has attempted to model the dynamics of invention mathematically by analysing specific knowledge spaces Tria et al. (2014), Loreto et al. (2016), Thurner et al. (2010), Klimek et al. (2010), Klimek et al. (2012), Hidalgo and Hausmann (2009), Tacchella et al. (2012), Servedio et al. (2018), Kauffman (1993), Gabora (2013). The aim of these studies is not to explain why some entities produce more innovations than others (productivity), or what influences the ability of these entities to produce them, but how knowledge evolves in a mechanistic view. These studies have provided evidence for the existence of innovation bursts in national economies Thurner et al. (2010), Klimek et al. (2012), the rediscovery of publications leading to the emergence of new scientific fields Thurner et al. (2019), Van Raan (2004), and the novel combination of components as a source of everyday novelties Tria et al. (2014). Few attempts focused on explicitly quantifying exaptation, one notable exception being Andriani et al. (2017), where it is estimated that about 40% of pharmaceutical drugs have started as something else.

Similarly, many scientific discoveries find applications that are not foreseen from the outset. The scientific context is particularly relevant for the study of exaptation since it encompasses a variety of human activities where knowledge is frequently rediscovered and re-used. In scientific evolution processes, different disciplines may come together, "to tell one coherent interlocking story" Watson (2017), or a field may subdivide into new disciplines. Both may form the basis on which concepts can further recombine. The recent use of statistical physics to examine people's behaviour in crowds, traffic, or stock markets is an example of co-opting theories and techniques to the social sciences. Research on laser technologies Bonifati (2010), pharmaceuticals Andriani et al. (2017), and fibre optics Cattani (2005) keep expanding their scope of application in very diverse fields. This kind of repurposing may enhance (though not necessarily) the fitness of entities Gould and Vrba (1982). Exaptation in the context of science thus refers to a diversification logic, where publications build on an existing knowledge base and succeed in entering other fields by creating new scientific niches or sub-fields. We thus interpret exaptation in science as how research insights from publications in one field are co-opted (i.e. cited) by publications from different scientific domains.

To arrive at a formal understanding of exaptation in science and technology we start by briefly reviewing related perspectives on the origins of innovations.¹ We then attempt to detect the fingerprints of exaptation by using publication data indexed in the APS (American Physical Society) database, which contains over 450,000 articles in the field of physics. We use the direct citation network to construct clusters of publications that represent sub-fields of physics. Citations have been considered as a proxy for academic relevance, with citation-based indicators offering approximate information about the scientific impact of publications Sugimoto and Larivière (2018). We focus on seminal publications that initially appear in a given domain and later receive acknowledgements and new functions from other domains. The idea of func-

¹It is not our aim to provide an in-depth discussion and definition of the concepts of novelty, innovation, or invention, which can be found elsewhere Erwin and Krakauer (2004), Arthur (2007); these terms will be used interchangeably throughout this chapter.

tion is critical here because it reflects knowledge-use of specific research outcomes in different scientific contexts. By investigating the "citation paths" of individual publications across different domains, we quantify both their overall importance, as well as their impact on the structure of the field of physics as a whole.

The chapter is structured as follows. In Sect. 1, we introduce the concept of exaptation as a theoretical concept and clarify the scientific context in which we will use it in this chapter. In Sect. 2, we describe the data and the empirical approach. In Sect. 3, we present results. Finally, in Sect. 4, we conclude the chapter and summarise our results and proposal in this area of research.

1.1 Exaptation in Science and Technology

A growing number of scholars in the area of innovation theory propose exaptation as the ultimate source of novelty. They argue that exaptation can explain the emergence of markets, technologies, and technical functions Dew and Sarasvathy (2016), Cattani (2005), Andriani et al. (2017), Mokyr (1991). In their view, exaptation leads to technological speciation or the creation of technological niches Andriani and Cattani (2016). In technological speciation processes, new technology develops from the effective transfer of existing knowledge to a new situation, where the transferred knowledge is interpreted and exploited in new ways Cohen and Levinthal (1990). Famous cases that illustrate this pattern include Corning Inc., a company that used its long-standing experience on glass engineering to deliver ground-breaking fibreoptic work that has transformed the telecommunications landscape Watson (2017), or the microwave, which was discovered by chance through the repurposing of parts of a radar system Rosenman (1988). Often, a distinction is made between radical and incremental innovations. While radical innovations transform the technological landscape, incremental innovations are minor improvements in existing technologies Dewar and Dutton (1986). Exaptation has been associated with radical innovations leading to the creation of new technological niches Andriani and Cohen (2013). Most empirical studies of exaptation in those contexts have been limited to small-scale or narratives of specific technologies.

In the context of science, contributions to the study of invention have used scientific publications, and metadata, such as author affiliation, organisation, location, and citation linkages to assess novel research outputs. Citation network analysis has been used extensively. Uzzi et al. (2013) used co-citation linkages from publications in various fields to differentiate between typical and atypical co-citations. Atypical co-citations are papers that are rarely cited together. They found that high-impact publications were usually not those that had the most atypical or novel combination of ideas, nor those that used typical combinations of ideas, but papers that cite a mix of new and conventional ideas. This result implies that, while originality is a crucial feature of high-impact science, the building blocks for new ideas are often embodied in existing knowledge Uzzi et al. (2013). Further, papers with high novelty as measured by atypical combinations tend to be less cited at the start, but are more likely to be cited after several years after publication Stephan et al. (2017). Other studies, which highlight the role of recombining ideas in driving innovation, suggest that older, seminal works are more likely to inspire ground-breaking science Kuhn (1962).

The combination of different theories, fields, and tools is also central to interdisciplinary research Wagner et al. (2011). Interdisciplinarity is likely to lead to more 'innovative' research Thurner et al. (2019), which is associated with higher levels of citation impact Larivière et al. (2015). Furthermore, the citation influence of papers is enhanced by the thematic distance (i.e. cognitively different fields) from the articles they cite Klavans et al. (2013). Yet, such outputs often face more resistance than mainstream publications (i.e. publications drawing mainly on the knowledge of a single field), thus requiring more time to get recognised by the wider scientific community Thurner et al. (2019). This idea relates to the "first-mover" advantage where mediocre papers will often receive more citations early on, than a later excellent one Newman (2009). There is, however, conflicting evidence that interdisciplinary research obtains higher citation rates at the level of journals in natural and medical sciences Levitt and Thelwall (1984), research departments Rinia et al. (2002), and in the field of biomedicine Larivière and Gingras (2010). This evidence shows that the relationship between novel research—as defined by interdisciplinary combinations—and impact depends on the characteristics of the fields and type of analysis involved Larivière and Gingras (2010).

2 Methodology

To track scientific progress, we use the APS dataset APS (2020), which includes publications in the leading physics journals since 1893. Following Blondel et al. (2008), we apply the Louvain algorithm to design an alternative classification scheme that clusters the set of all publications (articles and reviews) in the APS between 1893 and 2017 into research areas. The method is based on first determining pairs of publications that cite one another, and second, on clustering publications into a research area. The procedure uses a directed citation network where nodes consist of publications and links consist of citations between publications. Each publication belongs to a unique research area. We disregard the direction of the links in the network and exclude publications without citations.

Figure 1 shows the distribution of cluster sizes. For several clusters the number of publications is very small. For practical reasons we excluded clusters that have less than 10 publications. This method allows us to examine the influence of publications that belong to a specific field on other papers pertaining to different fields. This information is essential to determine whether a paper has been co-opted by papers in another field. This also allows us to trace the bibliographic properties of the citing publications.



Fig. 1 Cluster size versus rank. The number of APS articles in a cluster as a function of the rank of the clusters. Clusters were detected by the Louvain algorithm applied to the citation network. We cluster all articles appeared in APS from 1893 to 2017. In our analysis, we remove the articles belonging to clusters with less than 10 articles. These removed clusters constitute a few percent of all articles

2.1 Quantifying Exaptation

To quantify the idea of functionality, we define a quantity that we call *forward* normalised entropy (FNE), S_i , of a generic article a_i . In Fig. 2, we consider the articles citing a_i (red circle), each belonging to a cluster, C_n , here we use all papers published in APS until 2017. Denoting by A_i the set of articles citing a_i and by C_n the clusters in the system, we define $p_{i,n} = |C_n \cap A_i|/|A_i|$. In other words, $p_{i,n}$ is the fraction of articles citing the reference article a_i , that belong to cluster C_n . We define the normalised forward entropy, S_i , as:

$$S_i = -\frac{1}{\log N_i} \sum_{n=1}^{N_i} p_{i,n} \log p_{i,n} , \qquad (1)$$

where N_i is the number of clusters for which $p_{i,n} > 0$. We call S_i a forward entropy because it is computed based on articles published after a_i and citing a_i .

It gives information on how heterogeneous the composition of the citing articles is in terms of cluster composition. If an article is cited by articles belonging to only one cluster, i.e. it belongs to a well-defined scientific field, $S_i = 0$. If a paper has $S_i = 1$, then its citations are uniformly distributed among different areas. Therefore, the forward entropy can be thought of as a score for interdisciplinary impact.

To estimate the effective number of clusters from which the paper a_i received citations, we consider the Inverse Participation Ratio (IPR) I_i of article a_i :



Fig. 2 Definition of normalised forward entropy cartoon. Circles represent published articles and arrows stand for citations. Only those articles and links are displayed, which are relevant for the entropy definition. The article a_i denoted with the large red circle cites four papers (blue circles at its left side) and has been cited by nine papers (green circles on its right side). These nine articles belong to three different clusters C_n depicted as orange ovals. Denoting with p_n the fraction of articles of cluster n in the whole citation pool of the red article, we have $p_1 = 1/3$, $p_2 = 2/9$ and $p_3 = 4/9$. According to Eq. (1), the normalised forward entropy is then $S_i = (-1/3 \log 1/3 - 2/9 \log 2/9 - 4/9 \log 4/9)/\log 3 \approx 0.966$. The IPR for a_i is $I_i \simeq 2.79$

$$I_i = \left(\sum_{n, p_{i,n} > 0} (p_{i,n})^{-2}\right)^{-1}.$$
 (2)

Its value approximates the number of effective clusters citing a_i . We calculate the forward entropy and IPR for every year, by considering only those articles published in a given year, and citing a_i . In this way, we can follow the trajectory of an article over time, keeping track of the scientific areas it belonged to.

3 Results

We considered all publications in the APS database until 2017 and selected the top 200 most cited ones. The reasons for using highly cited publications are both conceptual and pragmatic. First, we assume that exaptation results from the significant adoption or acknowledgement of a paper. This implies that a co-opted publication should have a high citation impact. Second, a large number of citations enhances the statistical significance of the results. To identify distinctive patterns of exaptation, we looked at the yearly number of citations versus the forward normalised entropy (FNE), S_i , and the IPR, I_i , for all articles. We present a few examples with a well-defined signature of exaptation.

Before that, let us clarify how this pattern should ideally look like. A good candidate article for exaptation, say a_{ex} , ideally belongs to a well-established field and is disciplinary in nature. If the paper initially received citations only by papers in the same scientific sub-field, then its FNE score, S_i , would be zero. We hypothesise that at some point in time, the number of citations to a_{ex} starts increasing and possibly remains in the same scientific sub-field. At a later stage, the article may start receiving citations by papers from other scientific sub-fields, causing S_i to increase. The very fact that papers are co-opted in another scientific sub-domain also brings more citations to a_{ex} . If the new citing domain is highly productive, i.e., with many published papers, then S_i may eventually decline, as most of the citations will now come from the new citing field, overshadowing the original one. Eventually, while the citation rate of the paper will start to decrease as a natural consequence of ageing, its FNE, on the contrary, may increase slightly as other fields may become interested in the article and grow in relative importance.

The paper *The band theory of graphite*, published in 1947 Wallace (1947) seems to follow the hypothesised pattern of exaptation. Before taking a closer look, let us first dig into the graphene background. Graphite is a material made up of carbon atoms arranged in parallel hexagonal layers. Like the diamond, it is an allotropic form of carbon. While graphite is a conductor at room temperature, the diamond is an insulator. To understand why the carbon atoms with different crystal geometries are conducting or insulating it is necessary to understand how electrons behave once an electrical potential is applied. One of the great success of quantum mechanics was the possibility to understand these phenomena. The electronic structure of simple materials became computable right after the formalism of quantum mechanics was established. The geometry of graphite suggests that its electronic properties can be incrementally determined by first analysing a single layer of carbon—what is today known as *graphene*—and then by considering the mutual interaction between layers. As Wallace wrote in his manuscript Wallace (1947):

Since the spacing of the lattice planes of graphite is large (3.37\AA) compared with the hexagonal spacing in the layer (1.42\AA) , a first approximation in the treatment of graphite may be obtained by neglecting the interactions between planes, and supposing that conduction takes place only in layers.

Wallace did not consider the possibility that a hexagonal layer of carbon atoms could exist by itself and used it as a mere tool to solve the "more complicated" problem for the three-dimensional graphite. As recently pointed out in a review essay on graphene Castro Neto (2009):

It was P. R. Wallace, who in 1946 wrote the first papers on the band structure of graphene and showed the unusual semi-metallic behaviour in this material (Wallace 1947). At that point in time, the thought of a purely 2D structure was a mere fantasy and Wallace's studies of graphene served him as a starting point to study graphite, a very important material for nuclear reactors in the post-World War II era.

Let us see now why the seminal paper of Wallace on graphene can be considered an example of exaptation according to the pattern highlighted above. Figure 3, shows two panels of the yearly number of citations versus the forward normalised entropy



Fig. 3 A typical pattern for exaptation of an important paper. Left: yearly number of citations vsersu the forward normalised entropy of the paper of Wallace (1947). Each circle represents a different year, and the time-evolution is marked with a colour code, from dark tones (older) to light ones (newer). The ideal dynamics of citations and entropy over time for an exapted paper is also depicted by a thick arrow. The paper starts in one field ($S_i = 0$), then is exapted in another field leading to an increase of S_i ; then, citations grow since the paper gets more popular while S_i decreases, since the new field prevails; eventually, the number of citations decreases as an ageing effect while S_i increases again, since the paper is rediscovered in the older field. Right: yearly number of citations versus IPR of Wallace (1947)

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Fig. 4 Word clouds of the two communities citing Wallace's paper. WordClouds (2020) were generated by merging all the titles belonging to the main two clusters citing the graphite/graphene article. Stop words, numbers and punctuation marks were removed. Font size is proportional to the logarithm of the number of occurrences of words. The composition of the main cluster (graphene) with 613 articles citing Wallace's graphite article Wallace (1947) is shown on the left; the second important cluster (electronic structure properties) with 33 articles is on the right

(FNE) S_i (left), and the IPR, I_i (right). The paper starts with a small number of citations and a very small FNE (bottom-left corner of the plot in the left panel). After that, the pattern follows a very peculiar "S-shaped" trajectory, mirroring the following three situations: (i) the adoption by another field leading to an increase of S_i , (ii) the growth in the number of citations while S_i decreases, (iii) the decrease of the number of citations while S_i increases again.

This suggests that Wallace's article that was meant to belong to the field of electronic structure properties (ESP), was later co-opted in the graphene research field. According to the cluster analysis, the ESP field contains approximately 12,000 articles and the much more recent graphene area contains about 5,000 articles. Despite the larger number of articles in ESP, Wallace's paper has been cited mostly by the graphene community (613 times), and much less from the ESP (33 times). The forward normalised entropy of this paper follows the exaptation pattern we assumed. Its IPR pattern (Fig. 3 (right panel)) demonstrates how it switched from the ESP to the graphene community. To visualise the differences between the two ESP and graphene communities, in Fig. 4 we show two word-clouds from the articles citing Wallace's paper: from the graphene community (left) and the ESP one (right).

We found 10 additional articles whose FNE and IPR patterns are similar to those of the graphite/graphene paper. Among those, we mention two notable examples, i.e. Motion of Electrons and Holes in Perturbed Periodic Fields Luttinger and Kohn (1955) and Quantized Hall Conductance in a Two-Dimensional Periodic Potential Thouless et al. (1982). A third article, that was not in the list of the most 200 cited papers but was highly cited from outside the APS, was chosen on the basis of our personal experience, Spin Echoes Hahn (1950). The first Luttinger and Kohn (1955), is mainly cited by articles belonging to two clusters, the "Quantum dots / Quantum wells" cluster (QDQW) and the ESP cluster. These clusters are denoted by id = 8 and id = 1 respectively, and their mutual importance is sketched in the plots on the right panels of Fig. 5. Note how after 1980, the ODOW cluster starts to become more important than ESP, so that Luttinger and Kohn (1955) acquires more importance in that field. A similar situation occurs with reference Thouless et al. (1982) (second row of the panel), where now the graphene cluster (id = 16) competes with the QDQW cluster. Interestingly, from year 2010 on, also the "Bose-Einstein condensate" cluster (id = 12) starts to get some importance.

The third paper on spin echoes was chosen since we expected its importance on Nuclear Magnetic Resonance (NMR) would become prominent in time (third row of the panel). We do not observe a clear NMR cluster in APS, rather we find an exaptation pattern, where the "Entanglement" cluster (id = 7) emerges on the detriment of the QDQW cluster (id = 8), as shown in the bottom right panel. We think that the NMR community cites this paper from outside the APS community, i.e. by papers not published by the APS journals.

Although not directly related to the problem of detecting exaptation in APS articles, it is worthwhile looking at the time evolution of the FNE and the IPR for review articles. We observe the same kind of pattern consistently in all highly cited APS review papers. As an example, we show the Chandrasekhar's review *Stochastic problems in physics and astronomy* Chandrasekhar (1943); the corresponding plots for FNE and IPR are reported in Fig. 6. Both FNE and IPR increase over time, witnessing the number of different scientific fields interested in the review. The manuscript itself Chandrasekhar (1943) features four chapters, the problem of random flights, the theory of the Brownian motion, probability after effects, and probability methods in stellar dynamics. The IPR value reaches the value four soon and oscillates around it in time. On the other hand, the FNE, after reaching its maximum value, starts to



Fig. 5 More examples of exaptation patterns. Three articles are shown: Luttinger and Kohn (1955), Thouless et al. (1982), Hahn (1950), one in each row. In the left and centre panels, we display their citation versus FNE and IPR, respectively. Patterns are similar to what was found in Fig. 3. In panels to the right, we show the time evolution of their cumulative citations in the respective clusters, whose id number is given in the legend. Their vertical order reflects their ranking in 2017, i.e. their relative importance in citing the selected paper

decrease, mainly because one citing field increases its importance over the others. The IPR and FNE behaviour of highly cited reviews is essentially different from the patterns found for co-opted articles presented in Figs. 5 and 3. This finding further reassures us of the robustness of the proposed indicators, as well as of the overall methodology.

4 Discussion

The concept of exaptation has not been appropriately quantified. Only very few systematic quantitative analyses are available in the literature. Here we focused on the exaptation phenomena in the framework of scientific progress as it can be observed in the APS article collection database. Our approach consists of looking for signatures of exaptation in the adoption (as reflected in citation patterns) of specific results by other scientific communities than the original scientific area of belonging. To make the analysis quantitative, we propose a method based on two main components:



Fig. 6 FNE and IPR pattern for a typical review article in APS. Review articles exhibit a distinctive dynamical behaviour slightly different than the exaptation patterns discussed in Figs. 3. and 5. Left: the forward normalised entropy increases quickly and remains at high values over time, while the number of citations per year grows. Right: the number of clusters citing a review article grows over time showing an increased interest in several sub-disciplines

clustering of publications based on citation relations, and two observables, the Forward Normalised Entropy (FNE) and the Inverse Participation Ratio (IPR). These measures allow to single out patterns that are related to the exaptation phenomena in scientific evolution.

The evolution of feathers is a classical example of exaptation. Feathers were initially adapted to protect against thermal excursions and were later co-opted for flying. As soon as birds learn to fly, their fitness improves since they have higher chances of surviving predators. We extend this reasoning with a thought experiment (*Gedankenexperiment*) to the exaptation of scientific knowledge, where citations represent the fitness and the inverse participation ratio represents the number of functions a publication acquires over time. The example of graphene constitutes a popular instance of exaptation in physics, particularly in contributing to the development of two related sub-fields, electronic structure properties, and graphene. It shows that the 'survival' of a field depends on how pre-existing concepts are re-used or applied by communities in new domains resulting in new functionalities.

These results should be seen as preliminary steps towards a quantitative theory of exaptation; they show that is in principle possible to quantify exaptation, once it becomes possible to get a quantitative handle on the evolving context of a field. A better theory of exaptation is necessary to explain how something emerges and evolves by exploring its *creative potential* Andriani and Cattani (2016). The creative potential has been described as the functional shift of a particular component that could open up an evolutionary path different from its original and perhaps intentional trajectory Andriani and Cattani (2016), Kauffman (1993). We think that this paper could stimulate a new wave of studies in this promising area of scientific research.

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