

Quantitative Analysis of Macroevolutionary Patterning in Technological Evolution: Bicycle Design from 1800 to 2000

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To appear in: S. Shennan, ed. (forthcoming) *Pattern and Process in Cultural Evolution*, UCLA Press

Submitted July 2006, Revised November 2006, Accepted December 2006

A recurring pattern in biological evolution is that increases in diversity (adaptive radiation) proceed by early diversification at higher taxonomic levels followed by later diversification at lower taxonomic levels. Kauffman has argued that this macroevolutionary pattern results from the increased cost of exploring distant locations in design space as evolution proceeds and is the expected outcome of any process of adaptive evolution irrespective of substrate (Kauffman 1995, p.205–6). Indeed, he asserts that the development of the bicycle is a good example of a human design history which matches the pattern of adaptive radiation very closely (Kauffman 1995, p.207). Van Nierop et al's (1997) analysis of the development of the bicycle suggests that Kauffman's claim may be correct, although they were not

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specifically concerned with how bicycle design space was searched. In this paper we develop a methodology which allows us to quantitatively evaluate Kauffman's claim. We follow Lyman and O'Brien (2000, pp.47–53) in making use of clade diversity statistics (Gould et al. 1977) to examine the exploration of technological design space. However, unlike Lyman and O'Brien, we build an explicit hierarchical taxonomy of designs in order to investigate design diversity across different taxonomic levels.

1 Adaptive radiation and the evolutionary search of design space

The relative rates of speciation and extinction have varied in the course of biological evolution. When they are approximately equal at any given taxonomic level there is little net gain or loss in diversity, but when speciation rates exceed extinction rates the diversity of life increases. The latter phenomenon is known as an 'adaptive radiation' and is usually associated with the colonisation of an empty ecological space. As Ridley (2004, p.644) notes, "adaptive radiations can occur at all taxonomic levels and on all geographical scales". For example, the so-called Cambrian 'explosion' produced many new phyla (the second highest taxonomic level) across much of the earth's surface (Gould 1989), while in contrast, Darwin famously documented an adaptive radiation of finches which produced new genera, species and subspecies (the lowest taxonomic levels) in the restricted area of the Galapagos islands (Begon et al. 1990, p.19). Irrespective of scale, adaptive radiation typically follows a pattern characterised by rapid evolutionary diversification into a broad set of higher taxonomic classes followed by 'filling in' at lower taxonomic levels. Thus, for instance, families diverge relatively soon after the appearance of the orders to which they belong and, in turn, genera diverge

soon after the appearance of their families (Kauffman 1995, p.200). This pattern of early high-level diversification later followed by lower-level diversification appears to be quite robust: even in the event of mass extinctions, evolution tends to produce new lower level taxa within the surviving higher taxa, but rarely new higher level taxa. For example, starting at circa 550 million years ago the Cambrian ‘explosion’ first established all the major animal body plans—and hence phyla—that have ever existed (figure 1) and subsequently produced a further increase in diversity at the lower taxonomic levels of class, order, family and so on (Gould 1989). A massive decrease in the diversity of life occurred during the Permian extinctions at circa 200 million years ago. Although there is some debate about whether any phyla became extinct (see Lewin 1988 contra Knoll and Carroll 1999), it does appear that the subsequent rebound in diversity occurred at lower taxonomic levels within existing phyla rather than in the creation of new phyla (Erwin et al. 1987).

Evolutionary biologists often explain the pattern of adaptive radiation in terms of the filling of the “ecological barrel” (Gould et al. 1977, pp.38–9). The basic idea is that a relatively empty ecological space offers the greatest opportunity for the evolution of new forms of life, but as that space fills up increasing competition reduces the probability of further diversification. It is important, however, to be aware of exactly what is—and what is not—being explained. Gould et al. (1977) invoke the barrel filling theory to explain early diversification, but not specifically early diversification at higher taxonomic levels. In fact Gould himself is careful to distinguish these two different phenomena, preferring the term ‘diversity’ to refer to numbers of species and the term ‘disparity’ to refer to numbers of “anatomical designs for life” (Gould 1989, p.49). Thus diversification at low taxonomic levels produces an increase in diversity, but little change in disparity, whereas diversification at higher taxonomic levels will also produce greater disparity. It is not

immediately apparent that empty ecological spaces offer the greatest potential for the evolution of widely divergent forms of life, indeed, one could equally well propose that radical new forms of life would be most likely to succeed precisely because they avoid competition in congested spaces. Erwin et al. (1987, p.1185) argue that the rapid increase in diversity displayed at the family level during the Cambrian ‘explosion’ “is best interpreted as a consequence of the invasion of relatively empty adaptive zones by higher level taxa; the families were exploiting open opportunities within adaptive spaces to which higher-level taxa had achieved access.” While this invocation of the barrel filling theory clearly acknowledges that diversification initially occurred at higher taxonomic levels, it nevertheless does nothing to explain that particular fact.

Kauffman (1993; 1995) builds on the work of Gould et al., Erwin et al. and others in two important ways. First, he attempts to explain why early diversification occurs specifically at higher taxonomic levels and, second, he attempts to investigate whether with this pattern is a general feature of evolution by natural selection, irrespective of substrate. To this end he models evolution by natural selection as a search algorithm which seeks maxima in a correlated fitness landscape. The latter can be conceived as a multi-dimensional space describing all possible designs, each location being associated with a fitness. Kauffman’s model can be tuned to alter the correlation between the fitness of adjacent locations: a high degree of correlation produces a ‘smooth’ landscape in which adjacent locations share similar fitness values, while a low degree of correlation produces a ‘rugged’ landscape in which adjacent locations may have quite different fitness values (Kauffman 1993, pp.40–45). On a rugged landscape simultaneous mutations effect a long-jump across design space to a location whose fitness may be very different (better or worse), whereas single mutations effect a much shorter jump to a location whose fitness is likely to be closer to that at the origin. Kauff-

man finds that the chance of finding fitter variants by long-jump adaptation rapidly declines as evolution proceeds (*ibid.*, pp.71–4). This in turn leads to him to propose that there are “three natural time scales” (*ibid.*, p.74) to adaptation: an early phase in which evolution occurs by long-jump to distant locations in design space, a middle phase in which further evolution occurs by short jumps that effect a kind of ‘hill climbing’ to the fittest variants within smaller regions of design space, and a late phase of relative stasis awaiting increasingly improbable long jumps to more distant locations.

As archaeologists interested in cultural (and particularly technological) evolution we are attracted to Kauffman’s model by its substrate neutrality and its explicit treatment of how design space is searched. He argues that both biological and technological evolution occur on moderately rugged landscapes because both involve finding compromise solutions in the face of conflicting constraints (Kauffman 1995, p.179). He goes on to suggest that the three phase sequence of adaptation observed in his substrate neutral model of evolution by natural selection mirrors very closely the macroevolutionary patterns observed in both biological and technological evolution: specifically in the Cambrian ‘explosion’ (Kauffman 1993, p.76) and in the design history of the bicycle (Kauffman 1995, p.202). In the case of the Cambrian ‘explosion’, Kauffman proposes that the initial efficacy of long-jump adaptation led to evolution alighting on or near fitness maxima so distant from one another in design space that the resulting life forms fall within different high-level taxa. However, it rapidly became more difficult to locate distant fitter maxima, so evolution increasingly proceeded by hill-climbing in the immediate vicinity of already occupied locations in design space, resulting in new life forms which fall within existing higher-level taxa, but represent new lower-level taxa. Kauffman suggests that the same explanation is applicable to the design history of the bicycle, which saw early diversification followed by standardisation

on a limited number of basic designs.

2 Bicycle evolution

Although there were various attempts to construct a viable human powered carriage from the late 17th Century onwards, the forerunner of the modern bicycle is generally considered to be Baron Karl von Drais' Laufmaschine (running machine), patented in 1818 and more commonly called a 'draisine' or 'velocipede' (Herlihy 2004, pp.15–27). Constructed largely of wood, this comprised little more than a saddle slung between two spoked wheels. The initial name 'running machine' was apt, since it had no mechanical drive and was propelled by the rider pushing his or her feet against the ground. Despite early enthusiasm, which included organised races and a London coach maker's proposal of a woman-specific model (*ibid.*, pp.37–38), the draisine never established a lasting market and became largely obsolete within a matter of years.

Over the next 50 years there were various attempts to improve on the draisine by adding some kind of mechanical drive. These designs had either 3 or 4 wheels and introduced a wide range of drive systems including a pre-wound spring, foot operated treadle drive, hand operated levers and hand operated rotary cranks (*ibid.*, pp.53–66). None made a huge impact until the introduction of the first pedal operated velocipede in the late 1860s. Often considered the first true bicycle, the 'boneshaker', which was probably invented by Pierre Lallement in 1862, was being produced in the thousands by 1867 (van Nierop et al. 1997, p.260). Although the frame and wheels bear some resemblance to the draisine, the boneshaker incorporated pedals directly connected to the front wheel by cranks. This was not, however, the only means of propulsion used in boneshakers; in the late 1860s Thomas McCall built bicycles in which foot operated treadles were connected to

the rear wheel by means of rods (Herlihy 2004, pp.66–71). Rapid improvements to the boneshaker included the introduction of metal frames, wire wheels and solid rubber tyres.

In the 1870s the boneshaker was largely replaced by the faster ‘high wheeler’, on which the rider sat atop a very large front wheel of 40 or more inches diameter. Although the high wheeler was more comfortable than the boneshaker, it was both more dangerous, because the rider would be thrown over the handlebars from a considerable height in the event of striking an obstacle, and also more difficult to mount (Herlihy 2004, p.167).

From the late 1870s throughout the 1880s there were numerous attempts to marry the speed of the high wheeler with greater safety. These included tricycles with large indirectly driven rear wheels, bicycles in which the large driving wheel was placed behind a smaller front wheel, ‘dwarf’ high wheelers in which drive through a slightly smaller diameter front wheel was geared, and various designs which greatly reduced the size of both wheels and employed a geared chain drive to the rear wheel (*ibid.*, p.200–251). By the early 1890s the latter had become by far the most popular design and already resembled the modern bicycle: a so-called ‘diamond’ frame with two equal size wheels, the front steerable and the rear driven via a chain from cranks mounted below and forward of the saddle. This basic configuration has remained dominant for over 100 years, despite the sporadic appearance of new designs such as the recumbent bicycle (although an early recumbent design dates from height of the bicycle boom in the late 1890s (*ibid.*, p.288).

What this necessarily concise history of bicycle design demonstrates is that the modern bicycle is not the result of a simple unilinear progression from the draisine (see also Pinch and Bijker 1990). Rather, it is one branch of a radiation in which many, but not all other branches became extinct (see figure 2). It is this

observation which lead Kauffman to suggest that the design history of the bicycle provides a good example of the similarity between technological and biological evolution in terms of how they search design space. Indeed, Kauffman's claim is that they are not just similar, but fundamentally the same (Kauffman 1995, p.203). Van Nierop et al. (1997) were inspired by Kauffman's claims to undertake a largely qualitative investigation of bicycle design history. They constructed a fitness landscape which depicts the changing fitness of different basic designs over time, where the fitness is given by the relative popularity of those designs (ibid., p.256). As can be seen from figure 3, this clearly demonstrates (despite its truncation at 1900) a waxing and waning of bicycle diversity which does indeed look very much like an adaptive radiation. Van Nierop et al. do not, however, pursue this specific point any further: they neither attempt a quantitative assessment of diversity per se, nor do they explicitly discuss how bicycle design space was searched. Instead, their primary interest lies in an engagement with Kauffman's wider framework for understanding dynamical systems; they seek to "clarify the following statement: that the patterns of co-evolving dynamic ecosystems, such as the bicycle–society system, show periods of stability, progressive complication, transitions with critical fluctuations to new states, and evolve to the edge of chaos to be maximally adaptive" (ibid. p.254). We are open to that possibility, but our ambition for this paper is to develop a quantitative method by which we might empirically demonstrate whether changing diversity in the course of bicycle design history really is like that seen in biological adaptive radiation.

3 Aims, assumptions and method

Our principal question is whether the history of bicycle design exhibits rapid diversification at higher taxonomic levels followed later by extinctions and/or diver-

sification at lower levels. If this is indeed the case then it would appear to support Kauffman's claim that technological evolution (at least in the case of some technologies) searches design space in the same way that biological evolution searches design space. Under these circumstances it might be appropriate to talk of bicycle 'evolution', but it is important to recognise that this does not require any assumption about exactly how such evolution occurs. Our question can be addressed without knowing whether bicycle designs can be ordered into monophyletic lineages or whether the degree of reticulation is so great as to render that impossible (see O'Brien and Lyman 2003, pp.104–5 for a useful discussion of reticulation in culture). Our only assumption is that bicycle design as a whole constitutes a monophyletic lineage, which simply means that we ignore the possible import of design elements from other technologies. Note also that, unlike Van Nierop et al., we are concerned only with the diversity of design, not the fitness of individual designs: for our purposes it makes no difference whether a particular design of bicycle was built just once, or mass produced in the thousands (except insofar as that may impact our knowledge of the design). Given these assumptions there are three main tasks involved in answering our principal question: the first is to map bicycle design space by constructing a taxonomy of bicycle designs; the second is to populate these taxonomic units according to the dates of the first and last known occurrences of specific designs; and the third is to investigate the changing diversity of extant taxa.

4 Bicycle design taxonomy

It is not immediately obvious how one should go about constructing a bicycle taxonomy. Van Nierop et al. (1997, fig.3) divide 'bicycles' into 3 and 4 wheelers with indirect transmission, 2 wheelers with indirect transmission and 2 wheelers with

direct transmission; they also make a further cross-cutting distinction between 2 wheelers with and without a ‘backbone’. For our purposes there are two problems with this scheme: the first is that it captures only a few dimensions of bicycle design space and the second is that it is essentially flat, so does not permit investigation of what happens at different taxonomic levels. Lyman and O’Brien’s (2000) investigation of how the design space occupied by portable radios was explored between 1920 and 1955 is no more helpful with regard to the second problem. They measured the changing diversity of radio design by assuming that the number of designs is correlated with the number of manufacturers (*ibid.*, p.55) rather than by attempting to explicitly map radio design space by constructing a taxonomy of radio designs.

We have chosen to build a phenetic aggregative hierarchical classification system similar in principle to that devised by Linnaeus for the classification of biological organisms. The advantage of such a system for our purposes is twofold. First, a phenetic system (one based upon observed similarities and differences of form rather than relations of descent—see O’Brien and Lyman 2003, pp.31–34 for an introduction) is not dependent on a particular mode of evolutionary character transmission and so does not require us to make any assumptions about whether bicycle designs can be organised into monophyletic lineages. Of course, a phenetic classification may align with a phylogenetic classification, as indeed the Linnaean system does to a considerable degree (Ridley 2004, pp.473), but whether a phylogenetic classification of bicycles is possible and if so whether it aligns with the taxonomy described below are questions which we are pursuing elsewhere. Second, an aggregative hierarchical classification system (see Valentine and May 1996, pp.26–29 for the properties of an aggregative hierarchy) allows us to analyse the changing occupancy of taxa across arbitrary levels, which is necessary to permit investigation of whether bicycle design space was initially explored by di-

versification across higher-level taxa. One further point to note is that a phenetic hierarchical system is not restricted to any particular kind of trait: in principle it should be possible to construct taxonomies based on bicycle morphology, technology (mechanical coupling, materials used, etc.) or, for example, social context of use. Again, this is an issue that we intend to address elsewhere.

The specific taxonomy used in this paper classifies bicycles according to their morphological and technological attributes, for example, the number of wheels, the type of transmission, which wheel is the drive wheel and so on (see table 1 for the complete list). The hierarchical ordering, i.e. the level at which a particular attribute is considered, is based on Wimsatt's (1986) notion of "generative entrenchment". The basic idea is that mutations occurring early in development cause many downstream changes and so are relatively unlikely to produce viable organisms, whereas mutations occurring progressively later in development cause progressively fewer downstream changes and so are more likely to produce viable organisms (Schank and Wimsatt 1987, pp.37–38). Consequently, aspects of an organism that are laid down early in development are said to have high generative entrenchment because they are less likely to be altered in the course of evolution. Kauffman (1993, p.77) argues that post-extinction increases in diversity occur at lower taxonomic levels because it is precisely the developmentally early and thus highly entrenched attributes of organisms which are used to differentiate them at higher taxonomic levels. Although expounded in a biological context, Wimsatt's model is equally applicable to any process that explores a design space in such a manner that early 'choices' constrain subsequent possibilities. This is clearly true of bicycles. For example, a bicycle whose pedals and cranks are not directly coupled to the driving wheel may have either a chain or shaft-based transmission, whereas a bicycle whose pedals and cranks are directly coupled to the driving wheel can have neither kind of transmission. Thus we argue that the choice be-

tween direct and indirect drive is more generatively entrenched than the choice of transmission method, which is why we make the former distinction at a higher taxonomic level than the latter. Similar logic has been applied to the hierarchical placement of all other attributes listed in table 1.

The second stage of our analysis populates the taxonomic units according to the dates of the first and last known occurrences of specific bicycle designs. In other words, we classify each bicycle design into the leaf taxa depicted in figure 4 and record the first and last known dates of production of that design. Note that since we are not explicitly concerned with design fitness we do not record how many individual manufacturers' designs fall within a given taxon, nor the quantities in which they were produced; for our purposes we simply need to know the duration when a given taxon was occupied by one or more bicycles. The data used to populate the taxonomy comprised published images of bicycles collected from the following sources: Bijker 1995; Caunter 1955; Dodge 1996; Herlihy 2004; van Nierop et al. 1997. The 199 images chosen all satisfy two criteria: clear visibility of the morphological and technological attributes and provision of dates of production and/or the date of the original image in the accompanying text. In cases where sources disagree about the production dates of the same bicycle the average start and end dates are used.

5 Chronological taxonomic diversity

The third stage of our analysis is an exploration of the chronological patterning in how bicycle species populate the design space represented by our taxonomy. For this purpose we follow Lyman and O'Brien (2000) in borrowing tools developed by palaeontologists for the study of biological macroevolution, specifically, clade diversity diagrams and the clade diversity statistic known as "centre of grav-

ity” (Gould et al. 1977, pp.26–7). The reader is referred to Lyman and O’Brien’s (2000, pp.47–53) work for a detailed introduction. Here we simply reiterate the basic concepts and explain why we prefer an alternative terminology. Clade diversity diagrams (e.g. figure 5) depict the number of taxa present within a higher taxon (e.g. genera within a family) during each of a chronologically ordered series of discrete temporal intervals. The label ‘clade diversity’ reflects the usual assumption in evolutionary biology that the higher taxon in question constitutes a monophyletic lineage. However, as already noted—and as was also the case in Lyman and O’Brien’s study of radios—we prefer not to make any assumption about the mode of bicycle evolution. We simply use these palaeontological tools to measure the diversity of designs within a given taxonomic level. Consequently, to prevent confusion, we prefer the term ‘chronological taxonomic diversity diagram’ to refer to the diagrams that we construct. In similar vein, we label the set of sub taxa within a given higher taxon a ‘taxonomic set’ rather than a ‘clade’. It is also worth noting that, although outwardly reminiscent of the ‘battleship curves’ traditionally used by archaeologists for seriation, chronological taxonomic diversity diagrams differ in that they depict the changing number of types rather than the changing number (or relative frequencies) of instances of a type (Lyman and O’Brien 2000, p.47).

The centre of gravity (CG) statistic was devised by Gould et al. (1977, p.26) to provide “a measure of the relative position in time of the mean diversity”. It is calculated by scaling the duration of the taxonomic set’s existence from zero at the time of origin to one at the time of extinction and then measuring the position of the mean diversity along this scale, where the diversity is the number of taxa present at each temporal interval. The utility of CG is that it can be used to discriminate (but see Kitchell and MacLeod 1988 and Gilinsky et al. 1989 regarding statistical significance) between three different macroevolutionary patterns: CG

< 0.5 indicates rapid diversification followed by extinctions, as represented by a bottom heavy clade diversity diagram such as figure 5 or a bottom heavy chronological taxonomic diversity diagram such as figure 6; $CG = 0.5$ indicates a steady rate of diversification followed by a steady rate of extinction, as represented by a symmetrical diagram; and $CG > 0.5$ indicates a relatively late increase in diversification, as represented by a top heavy clade diversity diagram or chronological taxonomic diversity diagram.

Using chronological taxonomic diversity diagrams and the CG statistic we can explore the chronological manner in which bicycle species populate the design space represented by our taxonomy and, in particular, whether that occurs differentially at higher versus lower taxonomic levels. The basic method involves counting the number of occupied leaf taxa within some specified range of taxonomic levels and then using this count to plot the appropriate chronological taxonomic diversity diagram(s) and to calculate value(s) of CG. For example, in an analysis of levels 0 to 3 we take the first temporal interval and count how many taxa at level 3 are occupied (or have sub-taxa which are occupied) by at least one bicycle design. We then back up the hierarchy to level 2 and count the number of taxa which are directly occupied; we do not count those that are occupied by sub-taxa at level 3 as these are already accounted for. This summation of occupied leaf taxa continues until we reach the specified starting level. The final count constitutes the taxonomic diversity for that temporal interval. The chronological pattern of diversity is obtained by repeating the process for all remaining temporal intervals. Note that in any given analysis the number of diagrams and the number of CG values is equal to the number of occupied taxa at the highest taxonomic level specified. Figure 6 shows the chronological taxonomic diversity diagram for taxonomic levels 0 (the root) to 5 (one removed from the deepest level). This particular analysis is broadly analogous to plotting a biological clade diversity di-

agram for genera within a kingdom, although it differs by the inclusion of leaf taxa at higher levels than the lowest specified (because our bicycle taxonomy is not of uniform depth) and by measuring the diversity of designs rather than the diversity of clades *sensu stricto*.

Table 2 shows the values of CG for all the ranges analysed, that is: levels 0–5, 1–5, 2–5 and 3–5. Figure 7 plots the mean value of CG for each range. Figure 6 shows that diversity across taxonomic levels 0–5 exhibits the bottom heavy macroevolutionary pattern associated with a biological adaptive radiation: early diversification followed, in this case, by extinction and relative stasis. This result, mirrored in the low CG of 0.378, suggests that there may well be similarities in the way that biological evolution and technological ‘evolution’ explore design space. Furthermore, inspection of our populated bicycle taxonomy reveals that this early diversification occurs at higher taxonomic levels. Figure 7 provides a preliminary indication that there may be a trend in which the mean value of CG increases across the taxonomic ranges 0–5, 1–5, 2–5 and 3–5 respectively. If so, then it would appear that the macroevolutionary pattern associated with the exploration of progressively smaller regions of design space, i.e. within progressively lower taxonomic classes, is decreasingly like that associated with adaptive radiation and increasingly like that associated with relatively equal rates of diversification and extinction. Although we do not make any claims about the precise nature of this trend (i.e. whether it is linear or otherwise) we do nevertheless tentatively interpret it as evidence that exploration of bicycle design space did indeed proceed initially by long-jump adaptation on a relatively rough fitness landscape and subsequently by hill-climbing on a smoother fitness landscape, as proposed by Kauffman.

It is worth emphasising that *individual* chronological taxonomic diversity diagrams or centre of gravity statistics do not directly measure both aspects of diversification relevant to our question: they can measure changes in diversity but

not changes in disparity. In other words, they can measure whether diversification occurs early or late, but not whether it occurs early at higher taxonomic levels and subsequently at lower taxonomic levels. For example, our chronological taxonomic diversity analysis across levels 0–5 can not by itself distinguish whether the occupied leaf taxa in a given chronological unit are relatively sparsely distributed across all three level 1 taxa or densely distributed in just one of those higher taxon. The question of whether diversification occurs at higher or lower taxonomic levels can only be addressed by chronological taxonomic diversity analysis if it is applied at multiple levels, as we have done here. A better approach would be to devise a metric that directly measures chronological variability in the distance between newly occupied locations in design space, in other a words a metric that directly measures disparity rather than just diversity—we will report on an attempt to do exactly this in a future paper.

6 Conclusion

The basic question posed at the outset of our investigation was whether the exploration of technological design space produces the kind of macroevolutionary patterns that are well documented in biological evolution. Given the results of our chronological taxonomic diversity analysis we tentatively conclude that it does, at least in the case of the bicycle. Furthermore, we suggest that this supports Kauffman’s previously untested assertion that both biological and technological evolution proceed by early diversification at higher taxonomic levels followed by later diversification at lower taxonomic levels. We do, however, caution against extrapolating too widely from bicycles to other technologies. In particular, it is possible that the fitness landscape associated with bicycle design has relatively few peaks compared with some other technologies because the requirement of a

close coupling with human anatomy and physiology provides an unusually severe constraint on the range of viable alternatives (see Minetti et al. 2001 for possible evidence for this). If so, we would not necessarily expect to see the dramatic homing in on a relatively small portion of design space replicated across all technologies.

Finally, it is worth reiterating that this paper is primarily about the exploration of design space, not the reconstruction of phylogeny. In that sense it has more in common with Lyman and O'Brien's analysis of radio diversity, or indeed Layton's (2000, pp.262–266) invocation of Kauffman's ideas in his discussion of the evolution of farm technology, than it does with many of the evolutionary analyses reported in recent collections such as Lipo et al's' (2005) *Mapping Our Ancestors* and Mace et al's' (2005) *The Evolution of Cultural Diversity: A Phylogenetic Approach*. Whether the evolutionary process driving the exploration of bicycle design space produces monophyletic lineages is interesting, but was not our concern here; rather we wanted to know whether that exploration occurs by breadth-first search, producing diversification at higher taxonomic levels (an increase in disparity), followed by extinctions and subsequent local search, leading to a reduction in taxonomic diversity (a decrease in disparity). For this reason we further developed Lyman and O'Brien's use of clade diversity statistics for the analysis of technological evolution by calculating them for different levels in a hierarchical taxonomy designed to map the design space populated by our artefacts (bicycles). This multi-level analysis is the principal methodological contribution offered in this paper.

7 Acknowledgements

We are grateful to the UK Arts and Humanities Research Council (AHRC) for funding Jay Venti's work on this project, initially through the AHRC Centre for the Evolutionary Analysis of Cultural Behaviour (CEACB) and latterly through the AHRC Centre for the Evolution of Cultural Diversity (CECD); James Steele kindly facilitated the latter. We would also like to thank Stephen Shennan and members of the CECD Culture Club for discussions which have helped hone our thinking. Mike O'Brien and Robert Layton provided a number of useful comments that helped us identify several possible sources of confusion in the presentation of our work. Needless to say, we are responsible for any remaining errors of omission or commission.

References

- Begon, M., Harper, J. L., and Townsend, C. R. (1990). *Ecology, Individuals Populations and Communities*. Blackwell Scientific Publications, Oxford, 2nd edition.
- Bijker, W. E. (1995). *Of Bicycles, Bakelites, and Bulbs: Toward a Theory of Sociotechnical Change*. MIT Press, Cambridge, Mass.
- Caunter, C. F. (1955). *The History and Development of Cycles as Illustrated by the Collection of Cycles in the Science Museum. Part 1, Historical Survey*. Her Majesty's Stationary Office, London.
- Dodge, P. (1996). *The Bicycle*. Flammarion, Paris.
- Erwin, D. H., Valentine, J. W., and J. John Sepkoski, J. (1987). A comparative

- study of diversification events: The early Paleozoic versus the Mesozoic. *Evolution*, 41:1177–1186.
- Gilinsky, N. L., Gould, S. J., and German, R. Z. (1989). Asymmetries of clade shape and the direction of evolutionary time. *Science*, 243:1613–1614.
- Gould, S. J. (1989). *Wonderful Life : The Burgess Shale and the Nature of History*. Vintage, London, paperback edition.
- Gould, S. J., Raup, D. M., J. John Sepkoski, J., Schopf, T. J. M., and Simberloff, D. S. (1977). The shape of evolution: A comparison of real and random clades. *Paleobiology*, 3:23–40.
- Herlihy, D. V. (2004). *Bicycle*. Yale University Press, New Haven and London.
- Kauffman, S. A. (1993). *The Origins of Order: Self-Organisation and Selection in Evolution*. Oxford University Press, New York, Oxford.
- Kauffman, S. A. (1995). *At Home in the Universe: The Search for the Laws of Self-Organization and Complexity*. Oxford University Press, Oxford.
- Kitchell, J. A. and MacLeod, N. (1988). Macroevolutionary interpretations of symmetry and synchronicity in the fossil record. *Science*, 240:1190–1193.
- Knoll, A. H. and Carroll, S. B. (1999). Early animal evolution: Emerging views from comparative biology and geology. *Science*, 284:2129–2137.
- Layton, R. (2000). *Anthropology and History in Franche-Comté*. Oxford University Press, Oxford.
- Lewin, R. (1988). A lopsided view of evolution. *Science*, 241:291.

- Lipo, C. P., O'Brien, M. J., Collard, M., and Shennan, S., editors (2005). *Mapping Our Ancestors: Phylogenetic Approaches in Anthropology and Prehistory*. Transaction Publishers, New Brunswick.
- Lyman, R. L. and O'Brien, M. J. (2000). Measuring and explaining change in artifact variation with clade-diversity diagrams. *Journal of Anthropological Archaeology*, 19:39–74.
- Mace, R., Holden, C. J., and Shennan, S., editors (2005). *The Evolution of Cultural Diversity: A Phylogenetic Approach*. UCL Press.
- Minetti, A. E., Pinkerton, J., and Zamparo, P. (2001). From bipedalism to bicyclism: Evolution in energetics and biomechanics of historic bicycles. *Proceedings of the Royal Society of London B*, 268:1351–1360.
- O'Brien, M. J. and Lyman, R. L. (2003). *Cladistics and Archaeology*. The University of Utah Press, Salt Lake City, Utah.
- Pinch, T. J. and Bijker, W. J. (1990). The social construction of facts and artefacts: Or how the sociology of science and the sociology of technology might benefit each other. In Bijker, W. J., Hughes, T. P., and Pinch, T. J., editors, *The Social Construction of Technological Systems*, pages 17–50. MIT Press, Cambridge, MA.
- Ridley, M. (2004). *Evolution*. Blackwell Publishing, Oxford, 3rd edition.
- Schank, J. C. and Wimsatt, W. C. (1987). Generative entrenchment and evolution. In Fine, A. and Machamer, P., editors, *Proceedings of the 1986 Biennial Meeting of the Philosophy of Science Association, Volume 2*, pages 33–60. Philosophy of Science Association, East Lansing, Michigan.

- Valentine, J. W. and May, C. L. (1996). Hierarchies in biology and paleontology. *Paleobiology*, 22:23–33.
- van Nierop, O. A., Blankendaal, A. C. M., and Overbeeke, C. J. (1997). The evolution of the bicycle: A dynamic systems approach. *Journal of Design History*, 3:253–267.
- Wimsatt, W. C. (1986). Developmental constraints, generative entrenchment, and the innate-acquired distinction. In Bechtel, W., editor, *Integrating Scientific Disciplines*, pages 185–208. Martinus-Nijhoff, Dordrecht.

Tables and figures

Table 1: Generatively entrenched bicycle classification system

Order	Feature Category	Feature Type	Code
1	Number of Wheels	4 wheels	C
		3 wheels	B
		2 wheels	A
2	Wheel configuration	2 front and 1 back	TO
		1 front and 2 back	OT
		Asymmetrical	AY
		In-line	IL
		Parallel	PL
3	Drive technique	Diagonal	DG
		Non mechanical	N
		Hand operated lever	H
		Foot operated pedals on crank	P
4	Drive transmission type	Foot operated treadle	T
		Direct	D
5	Drive geometry type	Indirect	I
		Front drive	F
		Rear drive	R
6	Transmission-linkage type	Side drive	S
		Gear and chain	G
		Gear and shaft	X
		Lever and crank	L
		Lever and gear	V
		Direct crank	Z

Table 2: Mean values of CG

Taxonomic levels	CG per taxonomic set	Mean CG
0-5	0.378	0.378
	0.429	
1-5	0.430	0.467
	0.542	
2-5	0.500	0.440
	0.434	
	0.542	
	NULL	
	0.375	
	0.374	
3-5	0.417	0.491
	0.5	
	0.402	
	0.617	
	0.500	
	NULL	
	0.425	
	0.500	
	NULL	
	NULL	
	0.542	
	0.500	
	0.500	
	NULL	
NULL		
NULL		
0.500		
0.389		
0.500		
0.500		
0.500		

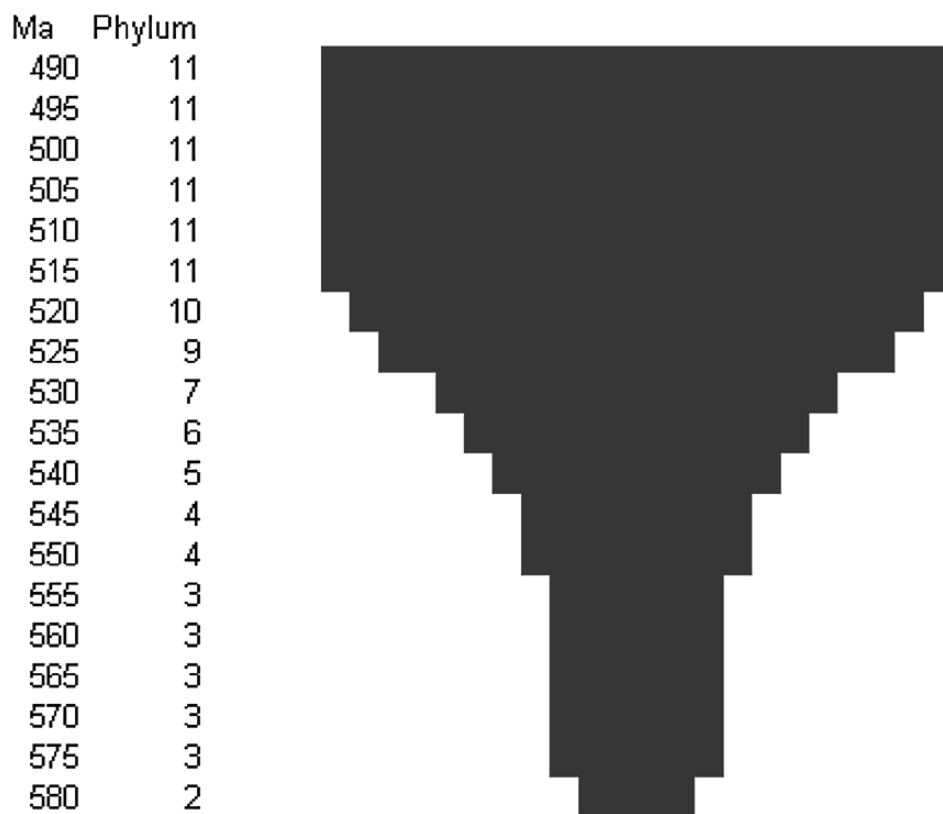


Figure 1: The Cambrian explosion produced many new phyla (data from Knoll and Carroll 1999).

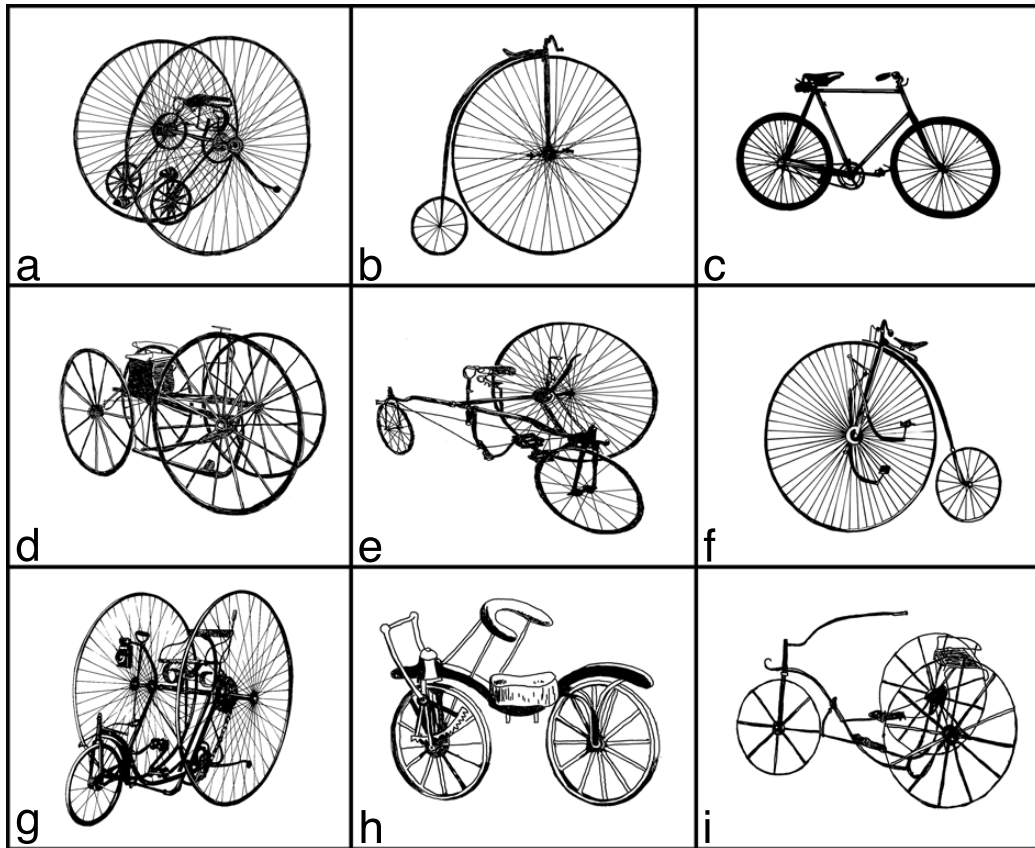


Figure 2: The diversity of early bicycle designs: a) Otto dicycle, 1881; b) Rudge ordinary bicycle, 1884 ; c) Osmond safety bicycle, 1896; d) Saywer's treadle-driven quadracycle, c. 1840; e) Starley's Coventry Rotary Tricycle, c. 1878; f) Singer Xtraordinary bicycle, 1878; g) Starley Royal Salvo tricycle, 1880; h) Gompertz' hand cranked draisine, 1821; i) Treadle-driven bicycle, c. 1850. Sources: a, b, c, f, g & i redrawn from Caunter 1955, plates I, IV, V, VI & X, by permission of HMSO; d & e redrawn by permission of Canada Science and Technology Museum; h) redrawn from *Polytechnisches Journal* June 1821.

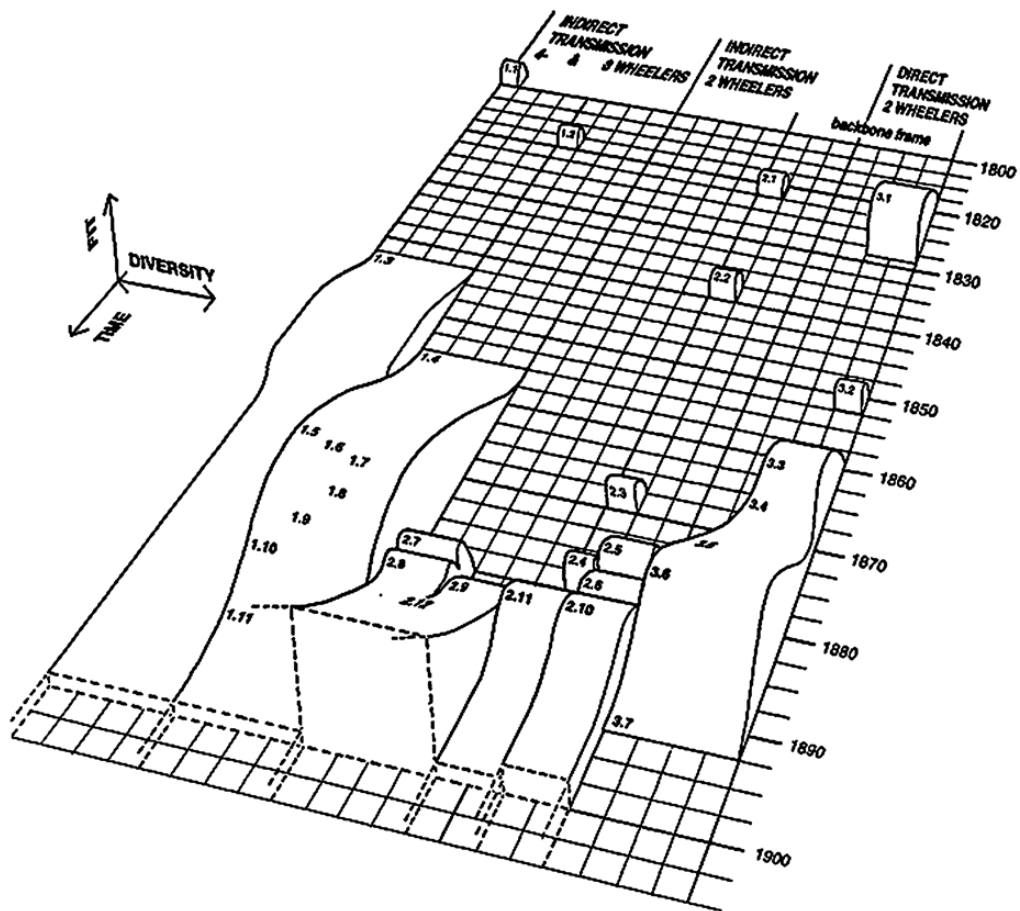


Figure 3: Van Nierop et als' model of changing bicycle design fitness (reproduced from van Nierop et al. 1997, fig. 3 by permission of Oxford University Press and the authors).

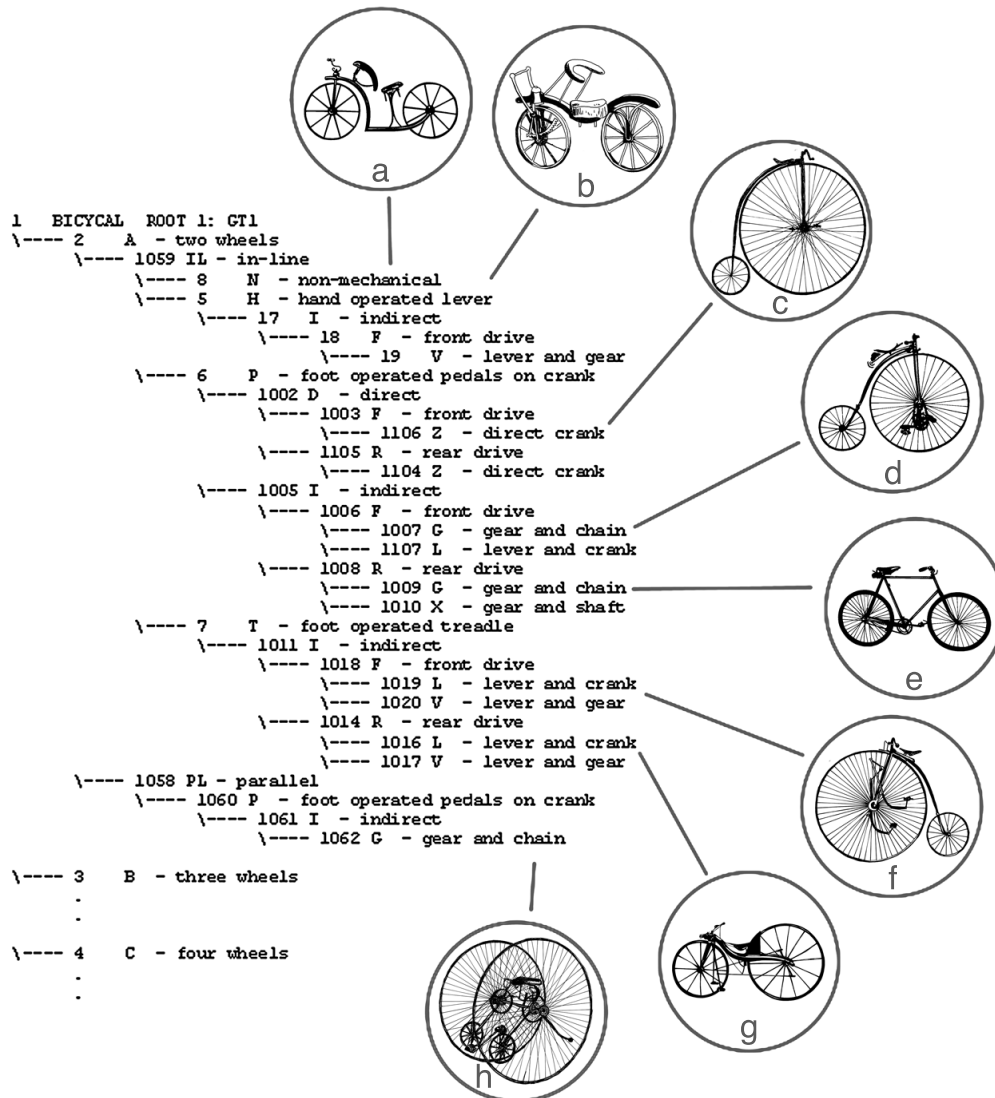


Figure 4: The bicycle design taxonomy with examples of leaf node occupants: a) Ladies' Hobby-Horse, 1819; b) Gompertz' hand cranked draisine, 1821; c) Rudge ordinary bicycle, 1884; d) Kangaroo bicycle, 1878; e) Osmond safety bicycle, 1896; f) Singer Xtraordinary bicycle, 1878; g) McCall's rear-driven bicycle, late 1860s; h) Otto dicycle, 1881. Sources: a, c, d, e, f, g & h redrawn from Caunter 1955, plates I, IV, V, VI & X, by permission of HMSO; b redrawn from *Polytechnisches Journal* June 1821.

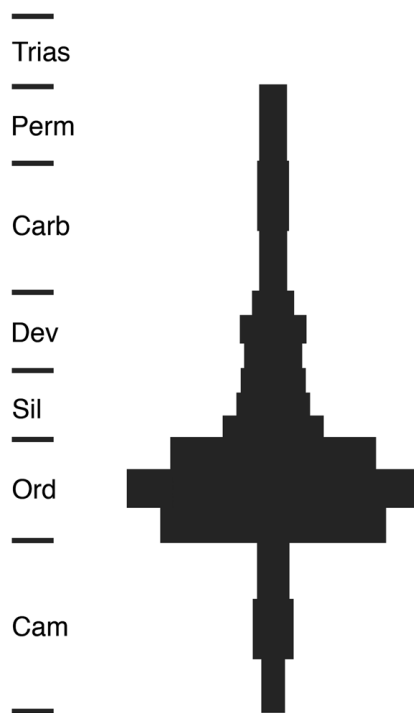


Figure 5: A biological clade diversity diagram showing the changing number of genera within the order *orthida* (drawn using data from Gould et al. 1977, fig. 1).

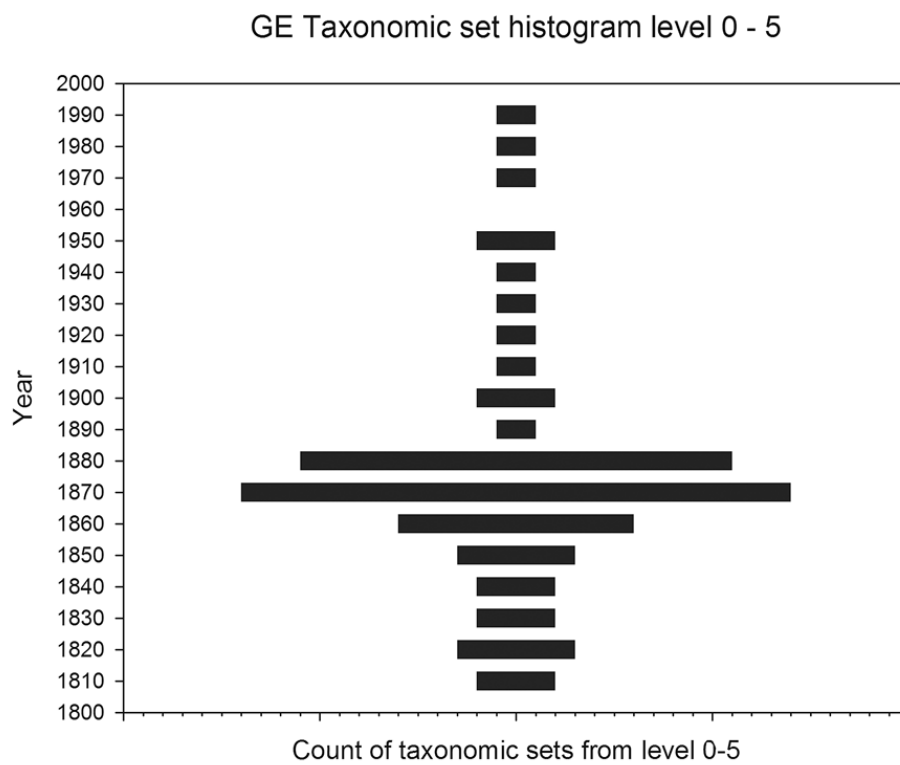


Figure 6: Chronological taxonomic diversity diagram for levels 0–5 of the generatively entrenched bicycle taxonomy.

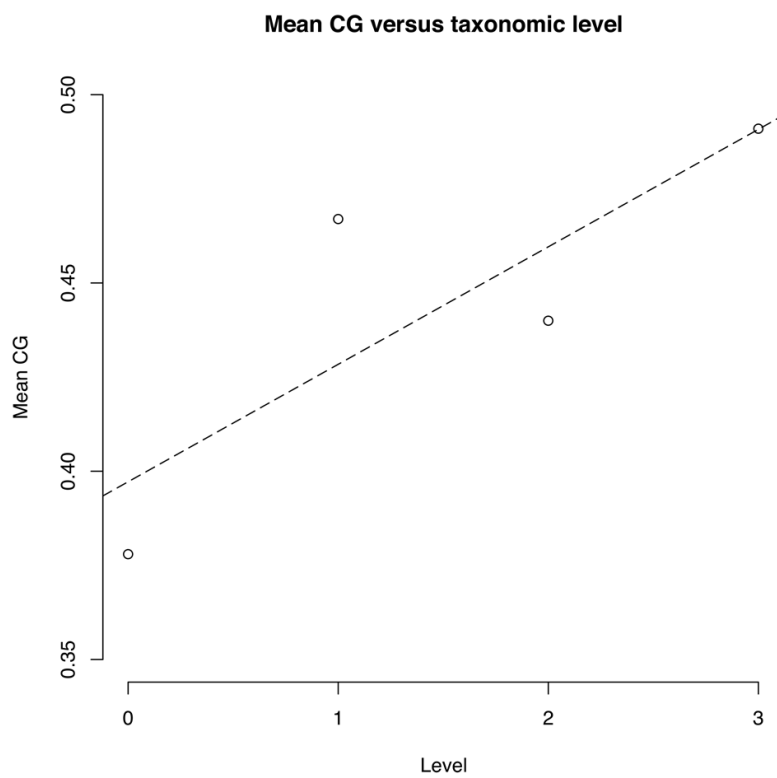


Figure 7: Linear regression on the mean value of CG for the following ranges of taxonomic levels: 0–5, 1–5, 2–5, 3–5 ($r^2 = 0.68$).