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Levels of selection in Darwin's *Origin of Species*

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Abstract References in Darwin's *Origin of Species* to competition between units of selection at and above the level of individual organisms are enumerated. In many cases these references clearly speak of natural selection and do not support the view that Darwin thought selection only occurred at the level of the individual organism. Darwin did see organismal selection as the main process by which varieties were created but he also espoused what is here termed community and varietal selection. He saw no essential difference between varieties and species and the references show that he also believed that selection could operate at the species level.

Keywords Darwin · Divergence · Evolution · Levels · Selection · Species

1 Introduction

In *The Origin of Species* of 1859 Charles Darwin explained his principle of natural selection which is today accepted as the main process of organic evolution. He said that every individual organism was slightly different from every other and since there were limits on the resources required to sustain life—thus leading to a struggle for existence—organisms with any advantageous characters would tend to leave more offspring. Darwin argued that natural selection, combined with what he called his principle of divergence, was sufficient to create diversity. He explained that in sexually-reproducing species, as varieties diverge they eventually become unable to interbreed. Once this happens there are two species where previously there had been one, and this is the process we now call speciation. Darwin was convinced "that Natural Selection has been the main but not exclusive means of modification"

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(1859, p. 6) and he grandly declared that by such means: "the forms of life throughout the universe become divided into groups subordinate to groups" (1859, p. 59).

Lewontin (1970) generalised the process of evolution by natural selection: "The generality of the principles of natural selection means that any entities in nature that have variation, reproduction, and heritability may evolve" and stated that "the principles can be applied to genes, organisms, populations, species, and at opposite ends of the scale, prebiotic molecules and ecosystems" (pp. 1–2). Brandon and Burian (1984) distinguished the 'units of selection', which are the entities selected (e.g. the gene) from the 'levels of selection', which are the entities at the level of which selection acts (e.g. the organism; see Gayon 1998, p. 421 Note 15).

The units of selection most usually thought of are the traits of individual organisms, with the corresponding level of selection being that of the organism. In the case of individual organisms, those with advantageous traits are today described as being better adapted and possessing superior fitness (i.e., they leave more offspring); their offspring inherit their parents' advantageous traits, thus changing the characteristics of the population and ultimately of the species. Individual organisms cannot themselves be units of selection as by definition they are not selected to survive into the next generation. No matter what the units are, however, for selection to drive non-random trends in evolution there will need to be some competition for resources, or more precisely there will need to be some common selection pressure which impacts on fitness at the appropriate level. In every case three conditions are necessary: firstly, the units must vary; secondly, there must be a process of transmission of the units to future generations; thirdly, there must be competition for resources (Pfennig and Pfennig 2012). Okasha (2006) has shown that, in principle, selection will apply to any unit which reproduces itself and which differs from and competes with other units at the same level so that some reproduce more than others.

Since life on Earth has evolved into nested hierarchies of self-reproducing units (e.g. organelles into cells, cells into organisms, organisms into species) we should expect selection to operate at all these levels, and often at several levels simultaneously. In recent decades there has been vigorous debate about how far up and down these hierarchies natural selection can actually be shown to operate. Weismann (1904) seems to have been the first to recognise selection operating below the level of the organism (his 'germinal' and 'histonal' levels), as well as at the organismal level ('personal') and above ('cormal'). He also clearly believed that selection could act on species and De Vries (1905) developed that idea and called it 'species selection'.

With the rise of Mendelian genetics in the first half of the twentieth century organism-level selection became accepted as the orthodox 'neo-Darwinian' explanation for evolution. The emergence of behavioural ecology around mid-century, however, revived interest in Darwin's idea that the individual organism might under certain circumstances sacrifice its own reproductive potential for the advantage of some higher level group to which it belonged, suggesting 'group' selection (Cronin 1991). In the last decades of the century palaeontologists also realised that their data on species origination, extinction and diversification might

challenge the hegemony of organism-centred Darwinism and this rekindled enthusiasm for De Vries's species selection (Gould 2002). Darwinism today seems to have expanded its dominion and has been invoked to explain selection down to the molecular level and up to the species level, but there is still confusion as to what Darwin himself actually said about levels of selection in *The Origin of Species* (here shortened to *Origin*).

It may be asked what might be gained from yet another study of Darwin's original formulation given that it was published 156 years ago? It is true that there is a considerable literature on Darwin's views in the context of contemporary debates on levels of selection. I would argue, however, that there is still room for a complete, rather than a selective, review of relevant passages in *Origin*. I hope to show from this that far from being the original 'organismal selectionist' of orthodox portrayal, Darwin actually saw selection driving evolution at all major levels higher in the hierarchy.

2 Levels of selection

The increasing complexity of life which has evolved on Earth has been largely due to the addition over time of levels to the hierarchy, driven by selection. Life must have started at the molecular level, then prokaryotic life and sex evolved and some forms coalesced into eukaryotic organisms; these in term grouped into multicellular organisms with differentiated tissues, interrelated as species, clades and ecological communities. Since most evolutionists are talking about multicellular organisms when they refer to organisms, the fact that such organisms are a 'late arrival' on Earth implies that suborganismal selection has been operating for billions of years, presumably since the origin of life itself.

As we move up the hierarchy from one level to the next, properties emerge from the 'whole' which are not simply the sum of the properties of the 'parts'. Also, as we move up, population size decreases, so that the number of varying units and hence the scope for selection decreases. The impact of this is presumably compensated by the fact that selection at higher levels must affect correspondingly larger numbers of units at the lower levels. Fitness at one level may or may not increase fitness at the next, for example altruistic behaviour may not confer fitness on the organism, but it may do so for closely related groups of such organisms. Sometimes selection at one level will appear to increase fitness for units at that level while decreasing it at higher levels, for example cancerous cells may kill the organisms that they 'need' for continuous self-reproduction.

Since the 1960s there have been debates about the levels at which natural selection operates. Interest has been mainly focussed on the issue of group selection within species, although as we shall see there remains confusion as to whether the term 'group' applies to one or several levels of selection. The contentious issues have been whether supraorganismal selection exists, if so how effective it is, and even whether the ontology of units and levels of selection has been rendered obsolete by the idea of the selfish gene (Hull 1981). I am not concerned here to trace these debates in detail as this has been done very ably by Dixon (2008) and by

Borrello (2010, 2013). Rather, my purpose is to define more precisely than hitherto Darwin's views on these issues, since there seems to be considerable uncertainty about this in the secondary literature. My interest is solely to understand Darwin's position, although to provide context I refer to the views of some other evolutionists, historians and philosophers of science.

Firstly, we should clarify the various meanings which have been applied to the terms 'group selection', 'kin selection' and 'interdemic selection' which have been applied in the supposed territory between the organismal level and the species level. A starting point is recognition that the most inclusive community of organisms which can all mate with each other is the species. Within a species there may be variant populations with distinctive traits which may have become isolated geographically or ecologically but which can still mate with other such populations if opportunity arises; these were termed 'varieties' by Darwin and are generally termed subspecies today.

Below variety level there are various forms of local populations generally termed 'demes' although their genetic and ecological boundaries are usually difficult to define. Populations may also form 'groups' with distinctive physiological or behavioural traits in which individual organisms appear to reduce their own reproductive success so that the group may prosper, as for example when resources are scarce, or to maintain some social hierarchy. Because such groups are generally small, poorly defined and do not have distinctive 'births' and 'deaths' it may be very difficult to prove that they constitute true units of selection. The smallest population unit is 'kin', composed of closely related family. The existence of sterile castes in social insects is often attributed to kin selection and seems to be linked to their unusual haplodiploid genetics in which females are more closely related to their sisters than to their offspring (Cronin 1991, 297).

We should now look briefly at the history of group selection theory. The idea of the 'altruist', that is an individual organism with traits advantageous to its group but disadvantageous to itself, was introduced by Darwin in *Origin* (never using that word) and developed by Haldane (1932). The important role of altruism in leading to group selection was strongly urged by Wynne-Edwards (1962) who argued that such selection could not be resolved downwards to the organismal level. On the other hand Wright (1931) introduced the concept of 'interdemic selection' which would act on conspecific groups larger than the immediate family while increasing fitness at the organism level and is thus quite different from Wynne-Edwards's concept. In Wright's model demes compete to exploit the available resources for the advantage of the organisms in the deme. Hamilton (1963) defined the more specific case of 'inclusive fitness' with selection acting on family groups consisting of very closely related individual organisms. Hamilton's 'kin selection' is sometimes seen as an extension of organismal selection because the fitness benefit still accrues to the individual, albeit via the reproductive success of its immediate relatives. Maynard-Smith (1976) argued that Wright's model should be called 'intrademic selection' as it is selection *within* and not between groups. In his important review he distinguished group (i.e., truly interdemic) from kin selection as separate alternatives.

The rise of population genetics in the early twentieth century led to a synthesis with natural selection theory to create a neo-Darwinian orthodoxy which heavily stressed organismal selection. In my view this was due to an overly narrow focus on anagenetic trends in conspecific populations under laboratory conditions (e.g. of *Drosophila*). This, again in my view, had the unfortunate effect of oversimplifying evolutionists' understanding of Darwin's own views and ultimately creating antagonism towards Wynne-Edwards's group selection. Williams (1966) while accepting the theoretical framework of multilevel selection (MLS) argued the principle of parsimony—that in identifying the level at which selection is acting one should never attribute it to any level higher than that for which one has evidence. He also argued that apparent group selection would usually be an effect of selection acting 'lower down', for example a herd of fleet deer appearing to be a fleet herd of deer. Ghiselin (1974) rejected group selection (see Sect. 4) while Williams went still further and advocated the view later developed by Dawkins (1976) that the gene may be the unit upon which selection is 'really' acting.

Less genetically minded biologists were attracted to the idea of group selection. Cronin (1991) drew attention to the increasing popularity of the group selection concept and what she termed 'good of the species' thinking among ecologists from the 1940s to 1970s. She contrasted it to orthodox organism-centred neo-Darwinism and she even linked it to the rise of holistic ideas such as Lovelock's 'Gaia hypothesis' of the Earth as a gigantic homeostatic organism (Lovelock 1979). Perhaps the most fruitful contribution to this approach has been the discipline of 'sociobiology' instigated by the world authority on ants, Edward Wilson (1975). Sociobiology synthesises genetical and ethological theory and has greatly aided understanding of the all-encompassing concept of MLS developed in particular by David Wilson (1980). This can be seen as an expansion of the theory of natural selection rather than as an argument against its efficacy.

Belief in the reality and efficacy of MLS depends on whether there are characteristics of the higher level units (e.g. population size, longevity in the fossil record) which are passed on to descendant units but which are not evolved by natural selection at the next lowest level. Evolution at the organism level (i.e., microevolution) is relatively easy to study in the field and laboratory. We must expect proving the reality and effectiveness of supraorganismal selection to become increasingly difficult as we move up the hierarchy of levels.

In addition to the continuing debates around group selection there has been, since the 1970s, increased interest in the reality and potential power of selection at the species level (Jablonski 2008). Empirical work on species selection is not easy because species are not physically bounded in the sense that organisms are, although they are bounded in time and by reproductive isolation. There are also formidable practical difficulties in studying interspecific competition in the field. So-called 'broad-sense' species selection, otherwise known as 'species sorting', may occur when the biological traits being selected reside at the organism level (e.g. body size), whereas 'strict sense' species selection may occur where the traits reside at the species level (e.g. geographic range). The complexity of the issues when just two living congeneric species are studied is amply demonstrated by the often-quoted 'ousting' from parts of Britain of the Eurasian red squirrel *Sciurus vulgaris* by the

introduced American grey squirrel *Sciurus carolinensis* (Collins et al. 2014). This example may have more to do with habitat destruction and comparative resistance to squirrel pox than to direct competition for resources, although of course disease resistance may certainly affect fitness at both the organismal and the species level. Even when selection in living clades is suspected it may be difficult to decide whether it is strict-sense species selection. It may also be extremely hard to prove, because of the impossibility of observing extinction and speciation which may require hundreds of thousands of years to occur.

Documentation of interspecific competition is almost impossible for fossils, as for example in the supposed competition between early species of *Homo*. Fossil species at least have the advantage of being available for tracking over geological time and palaeontologists have been eager to test the reality of species selection. Some, especially those (such as Stanley 1979) who believe strongly in the punctuated equilibrium model of speciation, are convinced that species selection is a significant contributor to the larger patterns in evolution (i.e., macroevolution). They argue that these grander-scale changes—more easily studied by examining the fossil record—are in fact effectively decoupled from microevolution. In Okasha's (2006) view, some documented palaeontological cases (e.g. in certain antelope and gastropod clades) are valid examples of species selection.

Okasha is certain that selection cannot operate above the species level because clades (i.e., groups composed of all the species with a single common origin) are incapable of reproducing themselves, given that by definition they include all their descendants. It remains to be demonstrated whether selection can be said in any meaningful way to apply to ecological communities (Lewontin 1970, p. 15).

3 Previous work on Darwin's levels of selection

In his important book on the role of sex in evolution Ghiselin (1974) praised Darwin for holding firm to a form of 'radical individualism': "Much as Copernicus moved the sun to the center of the solar system, Darwin placed the organism at the center of the biological universe" (1974, p. 17). Ghiselin applied this individualism, combined with a deep suspicion of altruism which he regarded as a 'metaphysical delusion', to an understanding of the economy of nature (1974, p. 25).

Ruse (1980), in his founding paper on Darwin's views on levels of selection, concluded that Darwin thought selection operated only at the organismal level, except in the case of humans where group selection might come into play in regard to the evolution of morality. It is important to note, however, that Ruse regarded Darwin as effectively including immediate 'family' in social insects as an extension of the organism. There is an issue here because Richards (1987) rejected this view, regarding Darwin's 'family' as a supraorganismal group. I return to this issue below.

Ruse's view of Darwin's position was supported in its essentials by Kottler (1985) and by Cronin (1991) who felt, however, that: "sadly, it seems that there can be no definitive answer as to what Darwin really had in mind" (1991, p. 306). Gayon's analysis of what Richards (1987) called Darwin's community level agreed

with Ruse's and he also rejected the possibility that Darwin believed in species selection. (Gayon 1998, pp. 70–73). He referred to Darwin's view as: "an extremely delicate question" (p. 68) and identified a subtle ambiguity in Darwin's wording where he might say something was 'for the good of the species' but was actually being delivered 'through the good of the individual'. Gayon's entire discussion of species selection actually concerns Darwin's rejection of natural selection as an explanation of hybrid sterility (see also Deen et al. 2013). This ignores the other issues at species and clade level discussed in Sect. 5 which in my view support an opposite interpretation. Gayon has more recently said less categorically that Darwin "almost completely rejected the notion of group selection" (2009, p. 293).

Gould (2002) accepted Ruse's view but also looked in some detail at how Darwin had dealt with the issue in his original 1856–1858 manuscript on natural selection but had been forced by circumstances to omit from *Origin*. Gould (2002) elaborated a comprehensive description of hierarchical selection theory, but his views concerning levels of selection in Darwin's writings have been challenged by Deen et al. (2013). Gould argued that Darwin strove to defend the centrality of organismal selection because he saw it as the very basis of his essentially gradualistic, uniformitarian theory. In Gould's view Darwin's was an uncompromisingly reductionist position regarding the level at which natural selection operated and: "Darwin's brave and single-minded insistence on the exclusivity of the organismic level, although rarely appreciated by his contemporaries, ranks as the most radical and distinctive feature of his theory" (2002, p. 14).

Gould believed that: "Darwin agonized over levels of selection" (2002, p. 50) while writing the section on divergence in his 'Big Book' on species (published from the manuscript and called *Natural Selection* by Stauffer 1975; see also Ospovat 1981; Hodge 2012). He argued that Darwin had made a special plea in *Natural Selection* that organismal selection would generate non-random trends at higher levels but, realising the weakness of his plea, excised it from *Origin*. Darwin's ad hoc argument was that extreme 'daughter' variants enjoy differential success, but they must somehow also retain the traits required to force extinction of their more 'generalist' parental variants, otherwise the net effect will be random, with no evolutionary trends. This was a biologically incoherent argument and would have been unnecessary if Darwin had been clearer that selection is here operating at the supraorganismal level. Darwin seems to have been unhappy with his position: "…but the subject is far too doubtful and speculative to be worth pursuing" (Stauffer 1975, p. 242).

In *Natural Selection* Darwin did invoke supraorganismal selection to explain how divergence cannot continue to absurdity, with every species eventually only having one individual. He gave three reasons why this never happens (not of course using modern terminology). Firstly, there is only a limited number of ecological niches available; secondly, variant populations cannot become too small because they will simply become extinct; thirdly, populations must have enough members to throw off variants for divergence to act on (Stauffer 1975, p. 248). The last two are aspects of supraorganismal selection at what I term the variety level.

Gould suggested that Darwin understood that macroevolutionary trends cannot be smoothly reduced to organismal selection but was forced by the arrival of Alfred

Russel Wallace's Ternate manuscript in 1858 to omit full discussion in *Origin*. Darwin's model in *Origin* has extreme variants, for example of an imaginary 'carnivorous quadruped' (p. 113), leaving more descendants, thus driving divergence of taxa and leading to such trends. I agree with Gould that Darwin recognised supraorganismal selection and struggled to understand its implications, but I disagree that he downplayed its role in evolution. In my view the entire ten-page 'caption' to the diagram in *Origin* (pp. 116–126) is clearly about divergence of varieties and species which share a common origin and as such is about supraorganismal selection; indeed, Darwin never explicitly mentions individual organisms in his discussion. Furthermore, in chapter ten of *Origin* (pp. 331–333) Darwin explicitly extended discussion of his diagram to cover not just species but groups of species. Bowler (1976) also seems to recognise that Darwin's discussion of divergence is about supraorganismal selection, though Bulmer (2005) apparently does not. For further discussion of Darwin's diagrams see Tammone (1995) and Kohn (2009).

Darwin began drafting what became *Origin* about a month after Wallace's manuscript arrived, but before that he allowed Charles Lyell and Joseph Hooker to publish some of his manuscripts alongside Wallace's as the first public announcement of the theory of natural selection (Darwin and Wallace 1958; see also van Wyhe 2013). Their joint paper was titled *On the tendency of species to form varieties; and on the perpetuation of varieties and species by natural means of selection*. Note that the word 'origin' does not appear in the title. Wallace sketched the principles of natural selection and explained how it might create a variety which eventually replaces the species from which it originated. His long last sentence states how this process might account for "all the phenomena presented by organised beings" but he never explicitly stated that natural selection accounts for the origin of new species. Darwin's contributions referred only to the origin of varieties and barely mentioned species, so it is perhaps not surprising that the paper had a rather "subdued" reception (Browne 2003, p. 40). Van Wyhe (2013, p. 215, Footnote 641) shows how in his section of the paper Wallace envisaged selection between 'varieties' but did not discriminate between varieties as individual organisms and varieties as races. Darwin and Wallace never again published together and the two men came to have fundamentally different understandings of levels of selection which I hope to explore in a future study. The most obvious difference between Darwin and Wallace on selection levels was Wallace's belief that hybrid sterility was a species-level adaptation, whereas Darwin saw it as a non-adaptive by-product of divergence.

Over the last decade more historians (Borrello 2010, 2013; Deen et al. 2013; Dixon 2008; Lustig 2009; Richards 1987, 2009; Sober 2011) have stated their view that Darwin did believe in various forms of supraorganismal selection. In his recent book, Elliott Sober (2011, p. 73) for example reads Darwin as espousing group selection, but he admits that Darwin's prose: "sometimes suggests otherwise". Borrello writes in connection with Darwin's work on social animals: "If these instincts are as important to the evolution of social groups as Darwin insists, and if the selection of these instincts often occurs at a level above that of the individual, then higher-level selection is an important factor in evolutionary theory" (2013, p. 348).

Sober summarises the issues raised by group selection and believes it to be a "legitimate hypothesis that sometimes is well supported by the evidence" (2011, p. 50). In respect of Darwin he says: "In almost all the examples that Darwin discusses, traits are said to be selected because they help the individual organisms that possess them to survive and reproduce" (2011, p. 18). Sober goes further: "as far as I know, Darwin never invoked the good of the species in his discussion of natural selection" (2011, p. 58). In fact Darwin does just that in several places (e.g. Darwin 1859, pp. 157–158, 200, 219, 224, 315); what he makes clear is that selection can never act only in the interests of *another* species. There are also many statements in *Origin* which show that Darwin believed that supraorganismal units, such as varieties and species, compete with each other, with some achieving dominance and others becoming extinct. In my view it is clear that Darwin sometimes thought this led to selection between these varieties and species, using the term selection as involving variation and inheritance. But we must be very careful when we read Darwin not to read only what we want to read with today's spectacles. As Sober puts it: "Darwin casts a long shadow, and many evolutionists have sought shelter in his penumbra" (2011, p. 50).

It may be asked where Darwin's principle of sexual selection fits into the picture. The principle was outlined in his 1844 'Essay' manuscript, then first published in chapter four of *Origin* and explained at length in *Descent of Man* (Darwin 1871; see Cronin 1991). Although sexual selection is crucial to organismal selection, it is not strictly relevant to the question of supraorganismal selection because sexes cannot reproduce themselves as separate units, except in the special case of parthenogenesis. Sexual selection while increasing organismal fitness might, however, increase vulnerability to extinction at the species level. This type of species selection has been termed 'Darwinian extinction' (Jablonski 2008, p. 508).

In summary, we can see that Darwin's account of natural selection in *Origin* was taken as more or less synonymous with organismal selection from the day it was published. This changed when Richards (1987) showed clearly that Darwin believed in selection of communities of social insects. This has provoked an unresolved debate amongst historians regarding precisely what Darwin meant partly because of his occasionally ambiguous wording but also because of selective quotation to support this or that view. Gould (2002) was the most strident advocate of the view of Darwin as strict organismal selectionist, only allowing an exception for the origin of human morality, but several scholars have more recently accepted Darwin as more of a group selectionist. Gould (2002) did great service in his exegesis of Darwin's principle of divergence, but on the basis of a complete survey of Darwin's text I argue below that Gould's account makes more sense if we accept Darwin as a multilevel selectionist.

4 What Darwin said on levels of selection

My purpose in this article is to take a fresh look at what Darwin said in *Origin* that is germane to the debates on levels of selection. I commence by enumerating the most obvious references in Darwin's text to levels of selection. I then attempt to distil

from these references or quotations an overall view of Darwin's understanding of levels of selection.

For the purpose of this study I use Darwin's own term *'**individual**'* for the organismal level. I also recognise two levels discussed by Darwin between the organism and the species, the lowest of which is the *'**community**'* (following Richards 1987). Here we must take care as some authors regard Darwin's 'community' as an extension of the organism and not really a supra-organismal level at all (e.g. Ruse, Gould). Richards (1987, p. 151 Note 85) points out that even though Darwin used 'family' as equivalent to 'community', he also knew that some ant communities could be composed of several families so his 'community' is not equivalent to 'kin' in the modern sense. This use of 'community' has nothing to do with multispecies ecological communities.

The next level up is *'**variety**'* and selection at this level has something in common with 'divergence selection' introduced by Kohn (2009). Of course we must remember that Darwin usually used the term 'variety' for races but also sometimes for smaller conspecific groups of distinctive individuals (see his definition in chapter two of *Origin*). There is no such difficulty with the term *'**species**'* for the highest level. We can take Darwin's species to be groups of organisms whose members can breed amongst themselves but not with members of other groups (*Origin,* 175). For discussion of Darwin's understanding of these terms see Sloan (2009b). I have avoided the term 'group' throughout as it has had such a confused history, as outlined in Sect. 2, and because Darwin uses it for groups of *species* which in the absence of anything better I call *'**clades**'* although, as I discuss in Sect. 5.5, strictly speaking there can be no such thing as clade selection.

I have used the first edition of *Origin* because in my view it is the clearest expression of Darwin's views (Hoquet 2013). The second edition of 1860, however, has a strong claim to be definitive and is available as an Oxford World's Classic. On 24 November 1859, publication day of the first edition, Darwin's publisher John Murray asked him to make corrections for a reprint which appeared on 7 January 1860. Most of the corrections were very minor and the pagination was identical although a few amendments were more important and a third quotation was added opposite the title page. The online variorum edition on http://darwin-online.org.uk/Variorum/?index.html shows that none of the changes significantly affect the quotes in this article except deletion of the famous 'whale bear' passage (Darwin 1859, p. 184).

There are relatively minor but occasionally significant changes in the later editions of *Origin*, and I refer to these where appropriate. I also refer in Sect. 5 to relevant statements in *Variation under domestication* of 1868 and in *Descent of Man* of 1871. I ignore, however, the other works in which Darwin wrote relevant material: the unpublished 'Sketch' of 1842 and 'Essay' of 1844 (both in Darwin and Wallace 1958) and *Natural Selection* (Stauffer 1975; the relevant passages are on pp. 188, 249, 272, 366–374). Finally, I ignore Darwin's notes and correspondence (the latter all now published up to 1874). I hope to analyse some of these materials in a future study.

The full title of Darwin's book itself contains a key phrase: *'On the origin of species by means of natural selection, or the preservation of favoured races in the*

struggle for life'. Murray asked Darwin to shorten the original (Stauffer 1975, p. 10) which included the word 'varieties' rather than 'races'. Darwin used the word 'race' quite frequently in his 1844 'Essay' and eleven times in *Origin* for varieties in the wild, including 'favoured individuals and races' on p. 467.

Quotations which in my view refer to levels of selection from *Origin* follow, grouped as best I can into individual, community, variety, species and clade. I have kept the quotations as short as possible but with sufficient context to identify them easily on Darwin online. The number at the start of each quotation is the chapter and page and I have emboldened the phrase which includes the level of selection.

4.1 Individual

3.61: … **profitable to an individual** of any species; 3.63: … **one individual** with another of the same species, or with the **individuals of distinct species**; 3.75: … be most severe between **the individuals** of the same species; 4.81:…that **individuals** having any advantage… procreating **their kind**?; 4.82:… in any way favoured **the individuals** …the varying **inhabitants**…; 4.83: …only for that of **the being** …; 4.84: …at the improvement of **each organic being** …; 4.92:…and those **individuals** which produced more and more pollen…; 4.95:…each profitable to **the preserved being**; 4.99: …with a distinct **individual** …of distinct **individuals of the same species.**; 4.127: …variations useful to **any organic being** …; 4.128: … less improved and intermediate **forms of life**.; 5.136: …**each individual** beetle …depend on whether a **greater number of individuals** were …; 5.142: … to preserve those **individuals** …; 5.148: it will **profit the individual**… decided advantage **to each successive individual** of the species; …**each individual Proteolepas** …; 5.149: …can act on each part **of each being,** solely through and for its advantage.; 5.154: … continued selection of **the individuals** …; 5.170: … beneficial to **the individual** …; 6.172: …**each new form** will tend … to exterminate, its own **less improved parent or other less-favoured forms**…; 6.194: …by the preservation of **individuals** with any favourable variation …; 7.233: each **profitable to the individual** …; 11.351: …so far as it **profits the individual** in its complex struggle for life.; 14.459: … innumerable slight variations, each **good for the individual possessor**.

4.2 Community

4.87: …adapt the structure of **each individual for the benefit of the community**… selection cannot… **for the good of another species;** 6.202–3: … stinging be **useful to the community**, it will fulfil all the requirements of natural selection… …thousands of drones, which are **utterly useless to the community** …instinctive hatred of the queen-bee…**for the good of the community**…**;** 7.235: …that **individual swarm** which wasted least honey …transmitted …instinct to **new swarms**…**;** 7.237: …selection may be applied **to the family, as well as to the individual**…**;** 7.238: …sterile condition … **advantageous to the community**: …the neuters … differ… divided into **two or even three castes**…; 7.241: … the

extreme forms, from being the **most useful to the community**…**;** 7.242: … division of labour in the **communities of ants**, by the means of natural selection.

4.3 Variety

3.75: In the case of **varieties** of the same species, the struggle … equally severe ….; 4.108: … **the most favoured or improved varieties** …much extinction of the **less improved forms**…the **various inhabitants** …;4.109: …each **selected and favoured form**… **less favoured forms**… **as new forms** are … being produced…; 4.110: The **forms** which stand in closest competition …it is the most **closely-allied forms,—varieties of the same species, and species of the same genus or of related genera**… come into the severest competition …**each new variety or species**… will generally press hardest **on its nearest kindred**…; 4.113: …**carnivorous quadruped**…its **varying descendants** seizing on places…; 5.141: How much **of the acclimatisation of species** …how much to the **natural selection of varieties** …is a very obscure question.; 6.176: …we shall have to **adapt two varieties**…; 6.177: …the **more common forms**… supplant the less common **forms.;** 6.184: …**a race of bears** being rendered, by natural selection… 14.461:…offspring of slightly **modified forms or varieties** …; 14.467: …**favoured individuals and races**… A grain … will determine **which individual** shall live …—**which variety or species** shall increase in number…**;** 14.470–471: New and **improved varieties** will inevitably supplant …**intermediate varieties**; and thus **species are rendered** … **distinct objects**.

4.4 Species

2.46: … of no **service or disservice to the species**…**;** 2.52: If **a variety were to flourish** so as to exceed in numbers **the parent species** … rank as the species, and **the species as the variety;** or … supplant and **exterminate the parent species**…**;** 2.53–54: …the **dominant species**… produce **well-marked varieties**…have to **struggle with the other inhabitants** … **the species which are already dominant** … enabled **their parents to become dominant** …; *Chapter heading p. 60*: …most severe **between individuals and varieties** of the same species; often severe **between species of the same genus**…; 3.76: … severe **between species of the same genus**… **most severe between allied forms**… why **one species has been victorious** …**;** 4.102: …**mere individual differences** suffice for the work….**if any one species** does not become modified…; 4.107: **new forms will have been more slowly formed**…living fossils…; 5.153: … natural selection **for the benefit of the species**.; 5.157-8: … in order **to fit the several species** to their several places …; 6.173: …allied **species have descended from a common parent**… and has supplanted… parent and all the **transitional varieties** …; 6.175: and as **these species are already defined objects**… 6.194:…natural selection, working for **the good of each being**…; 6.196**:** …no **advantage to the species**…; 6.200: Natural selection cannot possibly …**for the good of another species**…; 6.205: … Natural selection will produce **nothing in one species** … another … **useful to the owner**. … through the **competition of the inhabitants** …**;** 7.209: … for the **welfare of**

each species…might be **profitable to a species**…; 7.219: ….of **advantage to the species**; 7.224: …of **use to the species**; 10.315: …the **offspring of one species** to fill the exact place of **another species** …10.317:… two or three **varieties**… converted into **species,** which … produce …**other species**…; 10.320: … **each new species**, is produced and maintained …; 10.320–321: …**most severe**…, between the **forms which are most like each other** … **descendants of a species** … extermination of the **parent-species**; and if many new **forms** …the nearest allies of that species…; 10.321: …whether it be **species** belonging to the same … class, which **yield their places to other species** …; 10.325: **New species** are formed by **new varieties** arising… some **advantage over older forms**; 10.326**: Dominant species** …still more dominant species…; 10.331: …divergence …depends solely on **the descendants from a species** … seize on many and different places…; 10.337:… for **each new species** is formed … some advantage …**over other and preceding forms**… more recent and **victorious forms** of life…; 10.340: …will yield to the more **dominant forms**…; 10.344: thus **new sub-groups and groups** are formed. …the **species of the less vigorous groups**, …tend to become extinct together…; 12.402: …**if one species has any advantage** …it will …. supplant it; 13.412: … the less improved, and **preceding forms**.; 13.435: … profitable …to the **modified form;** 14.467–468: …individuals of the same species …the **struggle** … equally severe between the **varieties of the same species**, and next in severity between the **species of the same genus.**; 14.469: …adapting **each form** …; 14.475: **old forms** … supplanted by **new and improved forms**.; 14.489: … **widely-spread species**, …will ultimately prevail and **procreate new and dominant species.**

4.5 Clade

2.56: **large genera** have often come to their maxima….; 2.59: The **larger genera** thus tend to become larger… **the forms of life which are now dominant** tend to become still more …; 4.106:… the **new forms produced** on large areas… have been **victorious over many competitors**, …, will give rise to **most new varieties and species**…the **productions** of the smaller continent …; 4.116: **A set of animals**, with their organisation but **little diversified**, could hardly compete with **a set more perfectly diversified** …compete with **these well-pronounced orders**. …descendants of any one species will succeed …as they become more diversified …**other beings**.; 4.125–126: …through one form having some advantage over other forms …**One large group** will slowly conquer **another large group**… the **later and more highly perfected sub-groups**…to supplant and destroy **the earlier and less improved sub-groups**. Small and broken **groups and sub-groups** …to disappear.; 4.130:… **an animal** …connects by its affinities two large branches of life… been saved from fatal competition …; 5.152: …**groups of species have descended from other species**…; 6.201–2: The **endemic productions** … yielding before the …**plants and animals** introduced…; 10.327: The forms which …yield … to the new and victorious forms… allied in groups …as **new and improved groups** spread…, **old groups** will disappear; 11.377:…the tropical productions were in a suffering state …the more **vigorous and dominant temperate forms** … crossed the equator…

The frequencies of the terms Darwin used in *Origin* which can be understood to refer to potential units of selection are as follows (approximate numbers in parentheses): species (31), form (24), individual (20), variety (13), being (eight), community (six), genus (four), inhabitant, group (three each), sub-group, production, race, set, swarm (two each), kind, order, animal, quadruped, plant, flower, family, kindred, offspring, caste (one each). Since only entities which can be passed on to future generations can be units of selection, most of the terms used by Darwin in these quotations are not units, but they can all be more or less neatly grouped into the levels at which selection may act on them.

This enumeration ignores most of the sections on divergence (pp. 116–126, 331–333) which I discussed in Sect. 3, because they deal entirely with supraorganismal levels so that it is therefore difficult to extract discrete quotations from them. There are problems defining each of Darwin's terms, and it seems likely that he used those such as 'kind' and 'form' for different levels depending on the context.

5 Discussion

So far as I am aware, no-one has ever suggested that Darwin had any concept of sub-organismal selection and there seems to be no mention of this in *Origin*. The only reference I have found in Darwin's writings to sub-organismal units is in the second part of his chapter on "the provisional hypothesis of Pangenesis" in *Variation under domestication* where he conjectures tiny 'gemmules' as the agents of heredity, as for example in the last sentence of the chapter:

> Each living creature must be looked at as a microcosm—a little universe, formed of a host of self-propagating organisms, inconceivably minute and as numerous as the stars in heaven (1868, vol. 2, p. 404).

Darwin at various points in the chapter describes how gemmules are "thrown off" by cells throughout the body. They may be passed on to the next generation where they self-replicate, remain dormant, or perish depending on circumstances, thus implying some kind of selection.

5.1 Individual

There are many clear statements in *Origin* about how selection operates to alter traits at the 'individual' (i.e., organismal) level. Most of these are enumerated in Sect. 4 and require no further comment. There is a passage on p. 136 concerning the flightless beetles of Madeira, which follows a discussion of how many individuals in a group, when subjected to the same pressures, will gradually change their characteristics. The passage speaks beautifully for the process of organismal selection:

> For during thousands of successive generations each individual beetle which flew least… will have had the best chance of surviving from not being blown

> out to sea; and… those beetles which most readily took to flight will oftenest have been blown to sea and thus have been destroyed… For when a new insect first arrived on the island, the tendency of natural selection to enlarge or to reduce the wings, would depend on whether a greater number of individuals were saved by successfully battling with the winds, or by giving up the attempt and rarely or never flying (Darwin 1859, p. 136).

Another passage, from the fifth edition published 10 years later, is particularly useful for clarifying Darwin's meaning:

> It should be observed that, in the above illustration, I speak of the slimmest individual wolves, and not of any single strongly-marked variation having been preserved. In former editions of this work I sometimes spoke as if this latter alternative had frequently occurred. *I saw the great importance of individual differences*, and this led me fully to discuss the results of unconscious selection by man, which depends on the preservation of the better adapted or more valuable individuals, and on the destruction of the worst (Darwin 1869, pp. 103–104) *[emphasis added].*

The shift in Darwin's position in the fifth edition reflects his concern that organismal selection might not be as potent as he had thought in 1859. This shift was in response to Fleeming Jenkin's 1867 review of the fourth edition (see Vorzimmer 1970).

I am more concerned here to focus on references in *Origin* to units above the level of the organism. I have divided the supraorganismal but sub-specific levels into a lower 'community' and an upper 'variety' level. Although Darwin never made such a clear distinction I discuss the two levels separately as I believe they represent real differences in his thinking.

5.2 Community

The lower level consists of what Darwin variously termed in *Origin* the 'swarm', 'community', 'family' or 'caste' for groups he encountered among the social insects. Darwin's uses of these terms in chapter seven (e.g. Darwin 1859, pp. 202–203, 235–242) have been debated as possible cases of kin or group selection whereby fitness is conferred on the group, but not on the individual organism. As mentioned above, some authors have interpreted Darwin's 'community' as an extension of the organism and not a separate level. In my view that interpretation is flatly contradicted by the quote from p. 237:

> This difficulty, though appearing insuperable, is lessened, or, as I believe, disappears, when it is remembered that selection may be applied to the family, as well as to the individual, and may thus gain the desired end (Darwin 1859, p. 237).

Furthermore, Darwin clearly explained in the fifth edition and at greater length in *Descent of Man* how the community members, at least in social insects, are all related and share instincts and other communal traits which are subject to selection

at a level above that of the organism. I admit that these clearer statements post-date the first edition by quite a few years, but this is partly explained by Darwin's reluctance to discuss humans in 1859.

Community level selection first appears on p. 87 in chapter four of the first edition in relation to social insects:

> …it will adapt the structure of each individual for the benefit of the community; if each in consequence profits by the selected change. What natural selection cannot do, is to modify the structure of one species, without giving it any advantage, for the good of another species… (Darwin 1859, p. 87).[1]

The subject is then developed in chapters six and seven:

> …for if on the whole the power of stinging be useful to the community, it will fulfil all the requirements of natural selection, though it may cause the death of some few members. If we admire the truly wonderful power of scent by which the males of many insects find their females, can we admire the production for this single purpose of thousands of drones, which are utterly useless to the community for any other end, and which are ultimately slaughtered by their industrious and sterile sisters? It may be difficult, but we ought to admire the savage instinctive hatred of the queen-bee, which urges her instantly to destroy the young queens her daughters as soon as born, or to perish herself in the combat; for undoubtedly this is for the good of the community; and maternal love or maternal hatred, though the latter fortunately is most rare, is all the same to the inexorable principle of natural selection (Darwin 1859, pp. 202–203).

Darwin saw sterile female workers in social insects as the greatest theoretical difficulty he ever faced, not because they behaved altruistically but because there were in some species several markedly different forms or 'castes' of workers (see Cronin 1991). As Richards (1987) has shown it took Darwin years to figure out how this could be explained by natural selection; after all, how could sterile organisms ever gain selective advantage from their traits if they cannot reproduce? Darwin's solution was to take a step backwards and look at the advantage which might accrue to the sterile organisms' parents and grandparents. I read him in chapter seven as going to extraordinary lengths to argue that different castes of sterile workers can result from selection acting through the fertile members of the community, as best illustrated by a fairly extensive quotation:

> Thus I believe it has been with social insects: a slight modification of structure, or instinct, correlated with the sterile condition of certain members

[1] In the fifth edition (1869, p. 99) this became "…it will adapt the structure of each individual for the benefit of the whole community; if this in consequence profits by the selected change." In the sixth edition (1872, p. 67) the last phrase became "…if the community profits by the selected change." Richards (1987, p. 217, Note 82) believes that the version in the first edition "spoke only of individual selection" inasmuch as Darwin is there assuming that all the individuals in the community are closely related.

> of the community, has been advantageous to the community: consequently the fertile males and females of the same community flourished, and transmitted to their fertile offspring a tendency to produce sterile members having the same modification.[2] And I believe that this process has been repeated, until that prodigious amount of difference between the fertile and sterile females of the same species has been produced, which we see in many social insects.
>
> But we have not as yet touched on the climax of the difficulty; namely, the fact that the neuters of several ants differ, not only from the fertile females and males, but from each other, sometimes to an almost incredible degree, and are thus divided into two or even three castes. The castes, moreover, do not generally graduate into each other, but are perfectly well defined; being as distinct from each other, as are any two species of the same genus, or rather as any two genera of the same family (Darwin 1859, p. 238).

The argument that in social insects a trait can be selected if it benefits the community also applies to the male drones who serve no other function than to ensure that their queen is fertilised by another male (p. 202) and to the honey bee's sting, which may be suicidal to the bee when defending against certain attackers. Darwin suggested (p. 202) that the sting has been co-opted from an earlier function which presumably would not have killed the bee (the sting is a modified ovipositor, so is only possessed by females). He explained that it is in the community's interest for some individuals to risk suicide by using their sting when called upon to defend them all.

Nine years later, Darwin made a clear statement of his views on this form of community selection in *Variation under domestication:*

> With sterile neuter insects we have reason to believe that modifications in their structure have been slowly accumulated by natural selection, from an advantage having been thus indirectly given to the community to which they belonged over other communities of the same species (Darwin 1868, vol. 2, pp. 186–187).

Then 3 years after that in *Descent of Man*:

> With strictly social animals, natural selection sometimes acts indirectly on the individual, through the preservation of variations which are beneficial only to the community. A community including a large number of well-endowed individuals increases in number and is victorious over other and less well-endowed communities; although each separate member may gain no advantage over the other members of the same community (Darwin 1871, vol. 1, p. 155).

Whenever Darwin discussed 'sacrifice', 'advantage' or 'benefit', he in no way implied that the organisms themselves were making any kind of conscious choice,

[2] In the sixth edition (1872, p. 230) the first part of this quote became: "As with the varieties of the stock, so with social insects, selection has been applied to the family, and not to the individual, for the sake of gaining a serviceable end".

merely that in social insects natural selection will favour communities in which the individual organisms possess a certain behavioural trait. He explicitly stated "that of all the differences between man and the lower animals, the moral sense or conscience is by far the most important" (Darwin 1871, vol. 1, p. 70). He did, however, speculate that social insects displayed in their instinctive behaviour some of the same feelings as those felt by humans, a species never tackled in *Origin*, and that this might explain the origin of morality:

> It may be well first to premise that I do not wish to maintain that any strictly social animal, if its intellectual faculties were to become as active and as highly developed as in man, would acquire exactly the same moral sense as ours. In the same manner as various animals have some sense of beauty, though they admire widely different objects, so they might have a sense of right and wrong, though led by it to follow widely different lines of conduct. If, for instance, to take an extreme case, men were reared under precisely the same conditions as hive-bees, there can hardly be a doubt that our unmarried females would, like the worker-bees, think it a sacred duty to kill their brothers, and mothers would strive to kill their fertile daughters; and no one would think of interfering. Nevertheless the bee, or any other social animal, would in our supposed case gain, as it appears to me, some feeling of right and wrong, or a conscience (Darwin 1871, vol. 1, p. 73).

In *Descent of Man* Darwin discussed altruism in self-conscious humans, where self-sacrifice may become a more powerful driver than self-reproduction and is one of the distinctive characteristics of our own species:

> There can be no doubt that a tribe including many members who, from possessing in a high degree the spirit of patriotism, fidelity, obedience, courage, and sympathy, were always ready to give aid to each other and to sacrifice themselves for the common good, would be victorious over most other tribes; and this would be natural selection (Darwin 1871, vol. 1, p. 166).

Moral behaviour conferring fitness on groups of humans represents the evolution of a new unit of selection, namely the 'tribe'. Some scholars, while admitting that Darwin in this passage is discussing group selection, focus instead on his apparent failure to explain how selection might establish such altruistic behaviour in the group (Cronin 1991, p. 328). In my view the tribe shares the other characteristics of Darwin's communities, except that free will comes into play in the tribe.

In summary, Darwin had a clear concept of what comprises a community in social animals, including humans. It is a conspecific group of related animals sharing a suite of behavioural traits evolved in the interests of the group, sometimes against the interests of the individual. These traits may reflect "parental and filial affections", as most clearly expressed in *Descent of Man* (vol. 1, pp. 80–81) or more subtle social bonds in self-conscious species. Either way, Darwin saw that natural selection operates at community level.

5.3 Variety

I believe the only supraorganismal but subspecific unit recognised with any formality by Darwin is 'variety', which probably subsumes some informal terms such as 'form' and 'race'. Did Darwin recognise selection between varieties? There are numerous quotes which exemplify the struggle between varieties leading to changing proportions between varieties over time, including the long sections on the principle of divergence. The question is whether this struggle can result in changes in the characteristics of the units of selection at that level (i.e., the varieties) which are not smoothly reducible to changes in the units at lower levels. This would be natural selection but not what is generally understood as classical neo-Darwinism.

In my view there can be little doubt that the following quote from page 141 of *Origin* is proof that Darwin thought varietal selection could occur:

> How much of the acclimatisation of species to any peculiar climate is due to mere habit, and how much to the *natural selection* of varieties having different innate constitutions, and how much to both means combined, is a very obscure question (Darwin 1859, p. 141) *[emphasis added].*

A quote from chapter six introduces the principle of the need for exploitation of habitats which may already be occupied:

> Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural powers of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in its conditions) only by its varying descendants seizing on places at present occupied by other animals (Darwin 1859, p. 113).

In the above case Darwin seems to be talking about a supraorganismal level of selection, albeit without a clear reference to varieties, since there is variation, inheritance and competition. The famous "whale bear" quotation on the other hand certainly concerns a race, which is a synonym of variety:

> I can see no difficulty in a race of bears being rendered, by natural selection, more and more aquatic in their structure and habits, with larger and larger mouths, till a creature was produced as monstrous as a whale (Darwin 1859, p. 184).[3]

Unfortunately the parentheses make it impossible to be sure that Darwin is here referring to the race as the level of selection, since the selection may be operating at organismal level. Quotes from chapter fourteen surely, however, confirm Darwin's belief in selection at varietal level, for example:

> New and improved varieties will inevitably supplant and exterminate the older, less improved and intermediate varieties; and thus species are rendered to a large extent defined and distinct objects (Darwin 1859, pp. 470–471).

[3] This was deleted from the 1860 edition.

Finally, as in the sub-title of *Origin*, Darwin expressed varietal selection with perfect clarity on p. 467:

> In the preservation of favoured individuals and races, during the constantly-recurrent Struggle for Existence, we see the most powerful and ever-acting means of selection. A grain in the balance will determine which individual shall live and which shall die,—which variety or species shall increase in number, and which shall decrease, or finally become extinct (Darwin 1859, p. 467).

The remaining issue is whether varietal selection is the same as group selection? I think they are not synonymous because the term 'group' has been too poorly defined including, as it does for some authors, what Darwin generally called 'community'. As I explained at the end of Sect. 5.3, 'community' for Darwin had a precise meaning and only applied to related organisms in social animals which shared certain behavioural traits. 'Variety' for Darwin had a quite different meaning which he defined as an 'incipient species' and is a group of conspecifics sharing a suite of characters which are likely to be noticed by systematists. There is no instance in *Origin* where Darwin could be read as conflating 'variety' and 'community', given the implication of close-relatedness and distinctive behaviour in the latter, other than would exist anyway among all conspecifics.

5.4 Species

Darwin saw no fundamental difference between varieties and species, so we should now consider if he ever discussed species selection. As early as his student days Darwin knew that defining an individual organism was no simple matter in plants or in social and colonial animals (Sloan 2009a). During the *Beagle* voyage Darwin also entertained the idea that species have predetermined life spans somewhat analogous to individual organisms, although he soon abandoned that idea (Hodge 1983). I will attempt to show that in *Origin* he believed in the reality of selection acting on species so that in some sense this was a return to thinking of species as higher level individuals.

Sober (2011, p. 81) took the view that because species selection is about differential reproduction of species and not organisms, Darwin did not invoke it because he was unwilling to 'reconceptualise' his basic understanding of the way selection works. I do not see the evidence for this. Darwin several times used phrases such as 'service or disservice to the species', 'advantage to the species', 'good—or welfare—of the species' or 'use to the species', usually referring to a trait originally of no service which has since been seized on by natural selection. He also had a concept of species having varied powers of reproduction and therefore varying levels of fitness, although of course not expressed in those terms.

In *Origin* Darwin explained in chapter two how 'dominant' plant species are those most likely to yield varietal 'offspring' retaining their parents' advantageous traits perhaps with slight modification:

Hence it is the most flourishing, or, as they may be called, the dominant species,—those which range widely over the world, are the most diffused in their own country, and are the most numerous in individuals,—which oftenest produce well-marked varieties, or, as I consider them, incipient species. And this, perhaps, might have been anticipated; for, as varieties, in order to become in any degree permanent, necessarily have to struggle with the other inhabitants of the country, the species which are already dominant will be the most likely to yield offspring which, though in some slight degree modified, will still inherit those advantages that enabled their parents to become dominant over their compatriots (Darwin 1859, pp. 53–54).

Darwin clearly described competition between species:

…the struggle will generally be more severe between species of the same genus, when they come into competition with each other, than between species of distinct genera… the competition should be most severe between allied forms…but probably in no one case could we precisely say why one species has been victorious over another in the great battle of life (Darwin 1859, p. 76).

A large amount of inheritable and diversified variability is favourable, but I believe mere individual differences suffice for the work….if any one species does not become modified and improved in a corresponding degree with its competitors, it will soon be exterminated (Darwin 1859, p. 102).

…each new variety, and ultimately each new species, is produced and maintained by having some advantage over those with which it comes into competition; and the consequent extinction of less-favoured forms almost inevitably follows (Darwin 1859, p. 320).

We must not, however, assume that divergence of character is a necessary contingency; it depends solely on the descendants from a species being thus enabled to seize on many and different places in the economy of nature (Darwin 1859, p. 331).[4]

Undoubtedly if one species has any advantage whatever over another, in will in a very brief time wholly or in part supplant it…(Darwin 1859, p. 402).

As the individuals of the same species come in all respects into the closest competition with each other, the struggle will generally be most severe between them; it will be almost equally severe between the varieties of the same species, and next in severity between the species of the same genus (Darwin 1859, pp. 467–468).

Furthermore, it is clear that Darwin saw species as capable of reproduction:

[4] This is followed by the discussion of supraspecific divergence.

> …it will be the common and widely-spread species, belonging to the larger and dominant groups, which will ultimately prevail and procreate new and dominant species (Darwin 1859, p. 489).

Putting these three premises together—varying fitness, competition and differential reproductive success—I think we may reasonably infer that Darwin believed in species selection, although I have to admit that he rarely used the word 'selection' in this context.[5] Perhaps the clearest expression of the principle is in passages such as this one:

> …one species giving rise first to two or three varieties, these being slowly converted into species, which in their turn produce by equally slow steps other species, and so on, like the branching of a great tree from a single stem… (Darwin 1859, p. 317).

It is a strong claim that Darwin espoused species selection, albeit implicitly, but I believe it is justified by the quotes above and by those discussed below under clades. It seems to me from the quotes that Darwin understood interspecific variability and competition, combined with species' powers of 'procreation', perfectly well. It is of course important to keep in mind that a species does not itself evolve by species selection, any more than an individual organism evolves by organismal selection. If species selection is happening, it is the lineages of species and the clades to which they belong which are evolving.

5.5 Clade

As previously stated, Darwin's discussion of his principle of divergence in *Origin* is mainly concerned with the divergence of varieties. However, on page 120—in his diagram 'caption'—Darwin extended his discussion to the origin of species and higher taxa: "Thus, as I believe, species are multiplied and genera are formed" and on page 125 "I see no reason to limit the process of modification, as now explained, to the formation of genera alone", which leads into the following passage:

> One large group will slowly conquer another large group, reduce its numbers, and thus lessen its chance of further variation and improvement. Within the same large group, the later and more highly perfected sub-groups, from branching out and seizing on many new places in the polity of Nature, will constantly tend to supplant and destroy the earlier and less improved sub-groups. Small and broken groups and sub-groups will finally tend to disappear (Darwin 1859, pp. 125–126).

There is a further, more ambiguous, reference to competition at supraspecific level on page 130 and a more explicit statement on page 152:

> But on the view that groups of species have descended from other species, and have been modified through natural selection, I think we can obtain some light (Darwin 1859, p. 152).

[5] Exceptions being the quotes cited in 5.3 and 5.5 (Darwin 1859, p. 467, 152 respectively).

We must, however, take care when interpreting such statements as macroevolutionary, because the fact that species may be "modified through natural selection" could mean either that organismal selection has modified each individual species or that the group has been modified by species selection.

In chapter ten Darwin appears as comfortable applying his principle of divergence to species and supraspecific groups as he is to varieties in chapter four:

> The forms which are beaten and which yield their places to the new and victorious forms, will generally be allied in groups, from inheriting some inferiority in common; and therefore as new and improved groups spread throughout the world, old groups will disappear from the world; and the succession of forms in both ways will everywhere tend to correspond (Darwin 1859, p. 327).

And in chapter eleven Darwin describes what might have happened to groups of plants during the 'Glacial Period' which reads almost like a military campaign:

> …the tropical productions were in a suffering state and could not have presented a firm front against intruders, that a certain number of the more vigorous and dominant temperate forms might have penetrated the native ranks and have reached or even crossed the equator… (Darwin 1859, p. 377).

So in these two quotes Darwin is expressing his view that groups of species can possess traits which might impact of their fitness in the sense of causing them to dominate or dwindle depending on the groups they compete with. It is not clear from the wording, however, whether or not Darwin sees these traits as the aggregates of those of the component species, or of some higher grouping.

Darwin's clearest discussion of competition between supraspecific groups concerns Australian mammals, where he states that the orders of 'our' (i.e., 'Europaeo-Asiatic') placental mammals are supplanting their previously isolated marsupial 'representatives'. His view is that the more intense competition in Europe has forced greater diversification of the placentals and given them a superior ability to occupy ecological stations formerly held by the relatively unspecialised marsupials:

> A set of animals, with their organisation but little diversified, could hardly compete with a set more perfectly diversified in structure. It may be doubted, for instance, whether the Australian marsupials, which are divided into groups differing but little from each other, and feebly representing, as Mr. Waterhouse and others have remarked, our carnivorous, ruminant, and rodent mammals, could successfully compete with these well-pronounced orders. In the Australian mammals, we see the process of diversification in an early and incomplete stage of development (Darwin 1859, p. 116).

And likewise with the fauna and flora of New Zealand:

> The endemic productions of New Zealand, for instance, are perfect one compared with another; but they are now rapidly yielding before the

advancing legions of plants and animals introduced from Europe (Darwin 1859, pp. 201–202).

Though these cases are clearly about macroevolution and in that sense decoupled from organismal selection, they cannot qualify as clade selection because, as Okasha (2006) showed, clades such as placentals—which by definition include all their descendants—cannot vary or reproduce. The kinds of shifting patterns of dominance within clades which Darwin is describing can best be understood as differential reproductive success due to species selection. While recognising that there is no such thing as clade selection, the evidence from *Origin* demonstrates Darwin's deep understanding of evolution at clade level and supports my contention that he implicitly espoused what we now call species selection.

6 Conclusions

There is little dispute that selection between individual organisms—classical Darwinism—is the core of Darwin's theory for the production of varieties which gradually become species, as exemplified by the quote on page 136 of *Origin.* The quote from the fifth edition (Darwin 1869, pp. 103–104) stresses that in earlier editions Darwin relied heavily on organismal selection. I know of no case in *Origin*, however, where Darwin ever said that selection can only work at that level. What I have been more concerned to do here is to decide whether in 1859 he believed selection operated at higher levels than the organism.

We have seen that Darwin explained certain characteristics of social insects as the result of selection at what I term community level. His concept of a community in social animals, including humans, is a group of related animals sharing a suite of behaviours evolved in the interests of the group, sometimes against the interests of the individual. It is at this level that some previous workers have identified Darwin as a 'group selectionist', although others have argued that the fitness benefit from community selection is still conferred at the organismal level. Surely this is a misreading of Darwin's numerous statements that the advantage accrues to the community allowing it to prosper at the expense of other communities.

'Variety' for Darwin is quite distinct from 'community' and for him meant a group of conspecifics sharing a suite of characters which are likely to be of taxonomic value. It is clear from a series of quotations that Darwin believed in selection operating at this level (e.g. *Origin,* p. 141) and this underpins his principle of divergence, which together with natural selection he regarded as the 'keystone' of his theory of evolution. Since 'the preservation of favoured races' will alter the traits of varieties within a species this must surely count as selection and is incompatible with the view that all evolution can be explained by selection between organisms.

In one instance near the very end of *Origin* (p. 489) Darwin referred to species as capable of procreation, which today we would say qualifies species as units of selection. He also saw species as competitors and recognised what we would today call varying degrees of fitness between species; this is clear from several quotations. I infer from a series of these that even though he rarely used the word selection in

this context he believed in selection at the species level and in my view the statement on p. 317 of *Origin* proves this.

Finally, we must acknowledge that Darwin saw competition operating at even higher levels, as with the orders of mammals in Australia. At this level macroevolutionary patterns are not reducible to organismal selection, but they are reducible to species selection. Although Darwin never used these terms I think there is ample evidence in *Origin* to demonstrate his profound understanding of the implications of species selection for macroevolution.

I conclude that it is incorrect to characterise Darwin's own view of natural selection as only operating at the organismal and community level. I go further than most previous workers in arguing that Darwin also had a clear understanding of selection at the variety and species levels. As expressed in *Origin*, the most important driver of evolution may be the tiny advantage that one organism enjoys over other member of its own species, but Darwin also saw clearly the power of natural selection all the way up the hierarchy of life.

For much of its history Darwinism has been synonymous with evolution within populations due to selection acting at the level of the organism. Only in recent decades have we realised that Darwin himself had a far more subtle and expansive understanding of the power of natural selection.

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