

FRONTIERS IN PALAEOLOGY

WHAT IS MACROEVOLUTION?

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Abstract: Definitions of macroevolution fall into three categories: (1) evolution of taxa of supraspecific rank; (2) evolution on the grand time-scale; and (3) evolution that is guided by sorting of interspecific variation (as opposed to sorting of intraspecific variation in microevolution). Here, it is argued that only definition 3 allows for a consistent separation of macroevolution and microevolution. Using this definition, speciation has both microevolutionary and macroevolutionary aspects: the process of morphological transformation is microevolutionary, but the variation among species that it produces is macroevolutionary, as is the rate at which speciation occurs. Selective agents may have differential effects on intraspecific and interspecific variation, with three possible situations: effect at one level only, effect at both levels with the same polarity but potentially different intensity, and effects that oppose between levels. Whereas the impact of all selective agents is direct in macroevolution, microevolution requires

intraspecific competition as a mediator between selective agents and evolutionary responses. This mediating role of intraspecific competition occurs in the presence of sexual reproduction and has therefore no analogue at the macroevolutionary level where species are the evolutionary units. Competition between species manifests both on the microevolutionary and macroevolutionary level, but with different effects. In microevolution, interspecific competition spurs evolutionary divergence, whereas it is a potential driver of extinction at the macroevolutionary level. Recasting the Red Queen hypothesis in a macroevolutionary framework suggests that the effects of interspecific competition result in a positive correlation between origination and extinction rates, confirming empirical observations herein referred to as Stanley's rule.

Key words: macroevolution, definition, species selection, competition, Red Queen hypothesis, extinction rates.

EVOLUTION can be studied from two decidedly different perspectives: the study of the processes that lead to evolutionary change and reproductive isolation within and among populations, and the study of the long-term fate of species or higher-rank taxa through geologic time. These two perspectives correspond broadly to two different disciplines (biology and palaeontology) and are usually referred to as microevolution and macroevolution. Yet, does this distinction indicate two operationally different levels of evolution or merely a difference between disciplines or scales? Different opinions about this question are reflected by different definitions of macroevolution, and conversely, different definitions imply different answers to it. In this context, the purpose of this paper is twofold. First, it explores existing definitions of macroevolution and asks how the choice of definition affects the categorization of evolutionary processes as either microevolutionary or macroevolutionary. Second, implications of a strictly conceptual definition of macroevolution are discussed with respect to the differential effect of selective agents at the microevolutionary versus macroevolutionary level. A focus

in this discussion is the role of competition, which demonstrates that evolutionary processes do not always operate analogously in microevolution and macroevolution.

DEFINITIONS

'It would be useful to define "macroevolution", but definitions vary.' (Futuyma 2015, p. 30)

Definition 1: Macroevolution as the evolution of taxa of supraspecific rank

The term 'macroevolution' was introduced by Philpitschenko (1927, p. 93), who referred it to the evolution of taxa above the species level in the Linnaean hierarchy (genera, families, orders, etc.) His motivation for distinguishing the evolution of higher-rank taxa from

‘micro’ evolution was the belief that major body plan modifications cannot arise through the summation of the small-scale changes on which Darwinian evolution is based. This view was very common at his time, and Philpitschenko’s (1927) book is mainly a review of existing work on the topic, with the purpose of setting an agenda for future research. Theoretical underpinning followed. Goldschmidt (1933) suggested that mutations that affect the rates of developmental processes could lead to sudden, saltational changes in the phenotype that are mostly detrimental, but in rare cases will produce ‘hopeful monsters, monsters which would start a new evolutionary line if fitting into some empty environmental niche’ (Goldschmidt 1933, p. 547). Later, Goldschmidt (1940) added to this developmental argument his idea of alterations in the chromosomal pattern as an explanatory mechanism for the postulated hopeful monsters, which catalysed partly polemic criticism of his concept in general (see Gould 2002, pp. 451–466 and Rieppel 2017, pp. 109–125 for detailed discussions). The modern assessment is more conciliatory and acknowledges some possible examples of hopeful monsters, mostly involving mutations of genes that regulate key developmental processes during ontogeny (e.g. Chouard 2010; Page *et al.* 2010; Rieppel 2017). This explanatory scenario is reminiscent of Goldschmidt’s (1933) original concept and led some researchers to the conclusion that evolutionary developmental biology (evo-devo) ‘clearly paved the way for a revival of saltational evolution’ (Theißen 2009, p. 46). (This potential for saltational evolution must be distinguished from a possible macroevolutionary role of developmental processes in biasing the production of variation, which is discussed below.) In spite of such rehabilitations, a definition of macroevolution as the saltational origin of new body plans caused by developmental genetic changes remains problematic. The reason is not so much that this process is theoretically impossible, but rather that developmental processes do not establish a qualitative break between two levels of evolutionary change (e.g. Arthur 2003; Hoekstra & Coyne 2007; Nunes *et al.* 2013; Futuyma 2015) that would allow for a consistent separation between microevolution and macroevolution.

In spite of the failure to identify a qualitative difference between the underlying processes, the distinction between microevolution and macroevolution based on the level of taxonomic observation persisted. The most common formulation that is still used today is that of macroevolution as ‘evolution above the species level’, which was probably popularized by the title of Rensch’s (1959) book. Originally referring solely to the evolution of characters that distinguish taxa above the species level, it is often referred today to patterns and causes of diversification of higher taxa, such as variation in diversity, speciation rates, and extinction among clades (Futuyma 2015, p. 30). If used in the latter sense, ‘evolution above the species level’ includes aspects of definitions 2 and 3

discussed below. Levinton’s (2001, 2012) definition of macroevolution as ‘the sum of those processes that explain the character state transitions that diagnose evolutionary differences of major taxonomic rank’ escaped from such ambiguity, but the problem of a clear distinction between microevolution and macroevolution under this definition persists. As Levinton (2001, p. 2) wrote: ‘It is not useful to distinguish sharply between microevolution and macroevolution’. This statement is true in the context of his above-cited definition of macroevolution, but it is also an admission of its inadequateness.

Definition 2: Macroevolution as a phenomenological term for evolution on the grand time-scale

When Dobzhansky (1937, p. 12) introduced the term ‘macroevolution’ to the English-speaking community, he added a time-perspective to the concept in saying that ‘macro-evolutionary changes ... require time on a geological scale’. After the rejection of the concept of macroevolution propagated by Goldschmidt (1940) and others, time-scale became an alternative basis for the definition of the term. For example, Dawkins (1982, p. 289) defined macroevolution as ‘the study of evolutionary changes that take place over a very large time-scale’ and added that the term should be used as a ‘neutral label’ unburdened by theory. Grantham (1995, p. 302) was more precise with regard to ‘time-scale’ by defining macroevolution ‘to be the domain of evolutionary phenomena that require time spans long enough to be studied using paleontological techniques’. These time-scale based definitions allow the incorporation of all processes that affect the long-term patterns of evolution, from biotic interactions to global environmental changes. This inclusiveness is the reason for their attractiveness as consensus definitions but, similar to definition 1, they do not provide clear-cut criteria for categorizing a given process as either microevolutionary or macroevolutionary. The vagueness in this respect results from the trivial fact that virtually all evolutionary processes, regardless of their magnitude, can at least theoretically sum-up over geologic time to gain relevance on the grand time-scale. Distinguishing macroevolution from microevolution by the scale of observation is therefore a convenient practice for designating different scopes within evolutionary research, but it remains diffuse as a definition and provides no basis for conceptual advances in the field.

Definition 3: Macroevolution as evolution that is guided by sorting of interspecific variation

The idea that species are units of selection dates back to de Vries (1905) and has reappeared independently several

times since then (see Gould 2002). However, it is fair to say that Stanley (1975) was the first to formulate a testable hypothesis on ‘species selection’ and to expound its consequences for the hierarchical structure of evolution. Accordingly, speciation decouples macroevolution from microevolution, and macroevolution is guided through differences in speciation and extinction rates. Subsequent research (e.g. Vrba & Gould 1986; Jablonski 2008a; and refs therein) distinguished between ‘strict sense species selection’, where selection occurs on traits that are emergent at the species level (e.g. geographical range), from ‘effect macroevolution’, which occurs by selection on aggregate organismic traits (Stanley’s original concept). If the focal level of selection is not specified, ‘species sorting’ has conventionally been used as a neutral term that avoids a statement about the causes for the differential success among species. Later, Lloyd & Gould (1993) and Gould (2002, pp. 656–673) regarded the ‘strict sense species selection’ concept (= ‘emergent character concept’ in their new terminology) as too restrictive. Instead, they argued that any pattern of differential speciation and extinction rates that correlates with a trait emergent at any hierarchical level is a case of species selection (‘emergent fitness concept’; see Lieberman & Vrba 2005 for further discussion). An important argument in favour of the ‘emergent fitness concept’ is that species selection acting on aggregate organismic traits can theoretically oppose selection at the organismic level and is therefore not reducible to this level (Grantham 1995). In this paper, I use ‘species selection’ in its broad sense based on the emergent fitness concept and refer to ‘species sorting’ when the term ‘selection’ appears inappropriate; e.g. in order to include cases of species drift or cases where the trait under selection is not heritable.

Stanley’s (1975) paper stimulated a vigorous discussion and plenty of subsequent research (see summaries in: Gould 2002; Jablonski 2008a, 2017a) but remarkably, it remained largely unnoticed that a substantial change in the scope of macroevolution was implicit in the new concept. Macroevolution according to the new concept no longer referred to the processes of morphological change that lead to evolutionarily new taxa of supraspecific rank (definition 1), but instead to the differential evolutionary success of clades through geologic time, caused by differences in speciation and extinction rates (Gould 1980, 1985). This change in scope is exemplified, among other things, by the different roles that speciation and extinction have in definitions 1 and 3. Most workers intuitively regard both speciation and extinction as macroevolutionary (including those who follow definition 1; e.g. Levinson 2001) but this practice is not in accordance with a strict interpretation of the different definitions. Under definition 1, speciation is potentially macroevolutionary (if it leads to species that establish evolutionarily new taxa

of supraspecific rank) but extinction is not, because extinction does not contribute to the evolution of new morphologies. Under definition 3, extinction is a central macroevolutionary process (analogous to death in microevolution; Stanley 1975), whereas speciation has both a microevolutionary and a macroevolutionary aspect. The process of morphological transformation between species is *always* microevolutionary (contrary to definition 1), because it occurs through selection among intraspecific variation. This also applies to punctuated equilibrium, which is sometimes seen incorrectly as a macroevolutionary model of speciation (e.g. Hoekstra & Coyne 2007). In contrast, the outcome of speciation as the source of interspecific variation is macroevolutionary, analogous to mutation and recombination as the source of variation in microevolution (Stanley 1975).

It should be noted that Stanley (1975, 1979) did not use species selection explicitly for defining macroevolution. Rather, he introduced his concept as ‘a theory of evolution above the species level’ (Stanley 1975) and thus as an explanatory model for macroevolutionary phenomena in the sense of existing definitions. Notably, Stanley’s (1979) textbook on macroevolution avoids a definition of the field, and species selection plays a surprisingly subordinate role in this work, although Stanley (1979, pp. ix–x) emphasized that ‘the species is the natural (if imperfect) unit of macroevolution’. Later, Gould (1980) linked macroevolution indirectly with species selection by defining it as the differential success among species, which is the obvious outcome of species selection (or sorting) and thus at least an implicit reference to that concept. I therefore regard species sorting as the essence of a third category among the existing definitions of macroevolution, although to my knowledge this has not yet been proposed explicitly.

Choice of definition

Currently, the neutral definition of macroevolution as evolution on the grand time-scale (definition 2) is most widely used, but this definition does not provide criteria for a consistent distinction between microevolutionary and macroevolutionary processes, which renders it conceptually useless. Referring macroevolution to the evolution of taxa of supraspecific rank (definition 1) has the advantage that it is in accordance with the original scope of macroevolution. However, it is undisputed today that all evolutionary change involves intraspecific modification, regardless of the quantity of the change, and that in this sense macroevolution would be indeed reducible to microevolution (e.g. Erwin 2000). Definition 3 is conceptually different from the original definition, but it allows the unequivocal distinction between microevolution

(where organisms are the units of sorting) and macroevolution (with species as units of sorting). Given the fundamental difference to the original definition, it would be desirable to introduce a new term for evolution that is guided by species sorting, but it is unlikely that a new nomenclature would find broad acceptance. I therefore suggest retaining the term macroevolution for evolution in the sense of definition 3, based on the concept of Stanley (1975) and others, and abandoning definitions 1 and 2. Because selection requires variation, I suggest the following formulation: *Macroevolution is evolutionary change that is guided by sorting of interspecific variation.*

Generation of variation: microevolutionary versus macroevolutionary aspects

Classic population-genetic models of microevolution or, more generally, natural selection as originally formulated by Darwin (1859), are based on the premise that intraspecific variation is ‘random’ in the sense that it is unrelated to the direction of evolutionary change (e.g. Gould 2002, p. 144). Stanley (1975) made a similar case for macroevolution by suggesting that speciation as the source of interspecific variation is random as well. These premises have been challenged by the recognition that developmental systems can impose a bias on the phenotypic variation on which selection operates at any level (e.g. Gerber 2014; Wagner 2014; Uller *et al.* 2018). There is currently no consensus about whether the impact of developmental systems on the non-random generation of variation can be accommodated within microevolution (e.g. Futuyma 2015) or constitute a different case that falls within the field of macroevolution (e.g. Erwin 2017; Jablonski 2017b; Uller *et al.* 2018). In the context of the definition of macroevolution advocated herein, as sorting of interspecific variation, biased production of interspecific variation can be seen as an analogue of sorting (corresponding to Erwin’s (2017) ‘developmental push’) that precedes species sorting by distributional processes, and might therefore be accommodated within macroevolution.

AGENTS OF SELECTION: MICROEVOLUTIONARY VERSUS MACROEVOLUTIONARY EFFECTS

Distinguishing microevolution and macroevolution by the level of sorting (organisms vs species) not only allows for a clear conceptual separation, it also puts emphasis on an aspect of evolution that is often ignored: the causes of evolution can only be understood if the effects of selective agents are analysed for both levels (e.g. Gould 2002;

Jablonski 2008a). Predation, for example, may cause microevolutionary changes within a prey species by placing individuals with certain antipredatory features at a selective advantage (situation 1 in Fig. 1A), or cause species selection by driving one prey species to extinction and another not (situation 2 in Fig. 1A), or have variable effects at both levels (Fig. 1B; see below for further explanations). Moreover, selection for a trait at one level can oppose selection for the same trait at another level (Grantham 1995; Jablonski 2008a). This section discusses the basic principles that underlie the differential impact of selective agents at the microevolutionary and macroevolutionary levels.

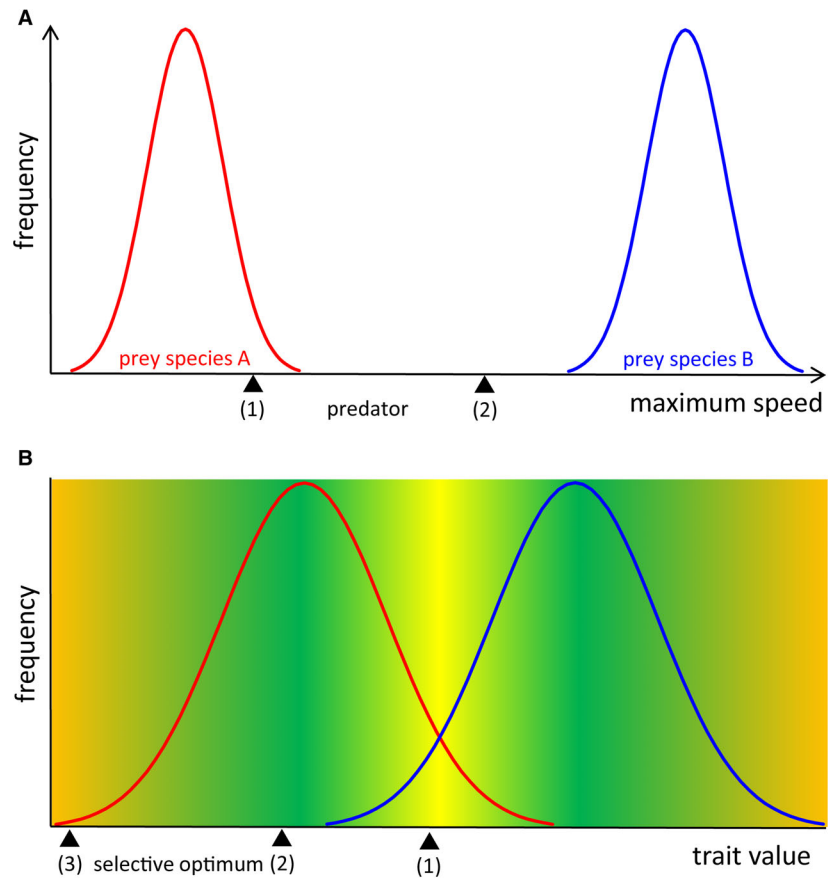
The answer to the question of whether selection occurs at the microevolutionary or macroevolutionary level is trivial in the case of ‘strict sense species selection’ (see Jablonski 2008a for a comprehensive overview), where the trait under selection resides exclusively at the level of the species, but not on the organismic level (e.g. sex ratio or geographical range). In such cases, selection occurs evidently only among interspecific variation; i.e. macroevolution.

The problem becomes more complicated if selection acts on traits that are variable between different organisms of a population *and* between different co-existing species, a situation that applies to most morphological, physiological or behavioural traits. A key requirement for a macroevolutionary effect of selection in this situation is that the trait under selection exhibits little or no variation within species relative to the variation among species (Jablonski 2008a).

Figure 1A–B illustrates how intra versus interspecific variation and the focus of selection with respect to these variations combine to either a microevolutionary or a macroevolutionary response. The common theme in both examples is that the focus of selection relative to the trait variation determines whether selection occurs within or between species.

In the first example (Fig. 1A), it is assumed that a predator appears in an ecosystem that contains two potential prey species A and B, and that the sole antipredatory strategy of these two species is escape. Equivalents of this simplified hypothetical case are invasive predatory species in present-day ecosystems (see Short *et al.* 2002 for some examples) or major evolutionary improvements of predatory skills in the geological past. In the illustrated case (Fig. 1A), the two different hunting speeds 1 and 2 of the predator with respect to intraspecific versus interspecific variation of the maximum escape speed of the potential prey species determine whether the effect of the predator on the prey is microevolutionary or macroevolutionary. Hunting speed 1 introduces a selection pressure favouring adaptations for faster running in the population of prey species A, because the hunting speed is within the range of the escape speed of some individuals of this species and these faster running individuals are at a selective advantage

FIG. 1. Microevolutionary versus macroevolutionary effects of selective agents. A, hypothetical case of a predator that appears in an ecosystem with two prey species; hunting speed 1 allows for a microevolutionary response of prey species A, whereas hunting speed 2 poses prey species B at a selective advantage over prey species A, which cannot respond by microevolutionary change; selection will therefore occur among interspecific variation (i.e. macroevolutionary) and potentially drive species A to extinction. B, overlapping variation of two species with respect to a relevant trait results in a fluent transition between three situations, depending on the focus of selection: (1) microevolutionary responses of both species (yellow, centre); (2) macroevolutionary response (green); and (3) macroevolutionary response plus microevolutionary response of the favoured species (orange); note that the fluent transition between the effects does not imply a transitions between the levels. See text for further details.



over slower individuals in the population. Hunting speed 1 therefore allows for a microevolutionary response of prey species A to the appearance of the predator; prey species B will remain unaffected because all of its individuals can escape easily from attacks of the predator. Prey species B will remain unaffected by the appearance of a predator with the higher hunting speed 2 as well, but in this case, species A cannot respond by microevolutionary change, because this hunting speed is far beyond the escape speed of its fastest individuals. In other words, species A lacks organisms that have a relevant selective advantage within the population and this prevents a microevolutionary response. Introduction of predator 2 will therefore lead to selection among the *interspecific* variation with respect to maximum escape speed of the two potential prey species and may drive prey species A to extinction; this is a macroevolutionary case. Gould (2002, p. 665) characterized this situation more generally: ‘The species doesn’t die because organism A, B, or C, possesses a trait that had become maladaptive; the species dies because none of its parts (organisms) can develop any other form of the trait – and this lack of variation characterizes the species, not any of its individuals.’

Distinction between microevolutionary and macroevolutionary effects is not always as clear-cut as in this example. Figure 1B illustrates a case in which the variation

within two species overlap with respect to a selectively relevant trait. Depending on the focus of selection, this situation results in a gradual transition between microevolutionary responses of both species (Fig. 1B, yellow area) and species selection that potentially eliminates one of them (Fig. 1B, green areas). If extreme trait values are selected for, a microevolutionary response of the favoured species will occur in addition to the macroevolutionary effect (Fig. 1B, orange). The crucial point in this example for understanding the rationale behind the micro/macroevolution divide is that the gradual transition between the *effects* on the microevolutionary and macroevolutionary level does not constitute a transition between these levels themselves. Rather, the relative effect of the selection pressure on either of these levels changes in response to its focus, whereas microevolution and macroevolution continue to operate independently.

COMPETITION IN MICROEVOLUTION AND MACROEVOLUTION

Competition occurs between individuals of the same species (intraspecific competition) as well as between individuals of different species (interspecific competition). An obvious and

operationally relevant difference between microevolution and macroevolution with respect to competition is that organisms (the microevolutionary case) can be subject to both intraspecific and interspecific competition, whereas species as evolutionary individuals (the macroevolutionary case) can only be subject to interspecific competition.

Intraspecific competition: mediator of selective agents in microevolution

Darwin (1859) addressed both intraspecific and interspecific competition without making an explicit operational difference between them, except from his repeated statements that competition is most severe between individuals of the same species (e.g. Darwin 1859, p. 75). However, a privileged role of *intraspecific* competition is implicit in his theory of natural selection, which in essence holds that intraspecific competition mediates between selective agents and evolutionary change through its effects on the representation of offspring in the next generation. Without intraspecific competition, there would be no microevolutionary response to any kind of selective pressures, including interspecific competition. This profound difference in the microevolutionary role of intraspecific and interspecific competition stands in contrast to the effects of competition on individual fitness, where it is irrelevant whether a conspecific or heterospecific competitor detracts from the resources of an organism.

Although intraspecific competition alone may promote speciation (e.g. Svanbäck & Bolnick 2007; Pfennig & Pfennig 2012), its momentum as a driver of evolutionary divergence is weak if it does not mediate external selective agents such as interspecific competition. This situation is exemplified in the aftermath of the end-Permian mass extinction, where diversification rates of many taxa remained extremely low for several million years because so many competing species had become extinct (Hautmann *et al.* 2015; Pietsch *et al.* 2018). Examples of intraspecific competition developing its own evolutionary dynamic do occur (Pfennig & Pfennig 2012) but if this internal dynamic is completely unrelated to the external environment (biotic or abiotic) its results might be negative at the macroevolutionary level. Cases in which increased organismic fitness increases species' vulnerability to extinction have been made in the context of sexual selection (e.g. McLain *et al.* 1999; Moen *et al.* 1999; Martins *et al.* 2018), which is obviously unrelated to any external agents of selection.

Interspecific competition: disentangling microevolutionary and macroevolutionary effects

In contrast to intraspecific competition, the principal effect of *interspecific* competition in *microevolution* is

promotion of niche differentiation and thus speciation (e.g. Mayr 1963; Schluter 1994; Emerson & Kolm 2005; Meyer & Kassen 2007; Pfennig & Pfennig 2012; Bailey *et al.* 2013; Calcagno *et al.* 2017). In this microevolutionary role, interspecific competition is the 'centrifugal force of evolution' (Mayr 1963), but it also contributes to the generation of interspecific variation that is subject to selection at the macroevolutionary level (Fig. 2). The prerequisite for a microevolutionary effect of interspecific competition is that variation of the trait under selection overlaps between competing species, as illustrated in Figure 1B.

In macroevolution, the outcome of interspecific competition is essentially binary, either causing displacement or extinction of the ill-adapted species, or permitting coexistence. In this aspect, interspecific competition does not differ from other selective agents in macroevolution. It should be noted, however, that the displacement/extinction alternative has opposing effects on biodiversity: extinction obviously causes a decrease in species richness, whereas geographical displacement may increase richness at the level of beta-diversity (Hautmann 2014). Interspecific competition might also affect rates of speciation, either negatively, by depressing population sizes of isolates and thus their probability of surviving to speciation, or positively, by causing local extinctions and so promoting allopatric speciation (Jablonski 2008b, p. 723).

Summarized (Table 1), competition in *microevolution* occurs: (1) as intraspecific competition, which has a central and unique role at this level in mediating between selective agents and evolutionary response; and (2) as interspecific competition, which is a main driver of evolutionary divergence. In contrast, competition in *macroevolution* manifests solely between species and affects coexisting species either directly by replacement, or it remains macroevolutionarily neutral (which, of course, does not exclude a potential microevolutionary effect). What is the ultimate cause of these differences in the role of competition in microevolution and macroevolution?

Intraspecific versus interspecific competition in microevolution and macroevolution

To answer this question, it is helpful to compare the role of *intraspecific* competition for change at the *microevolutionary* level with that of *interspecific* competition at the *macroevolutionary* level. Let us consider the differential responses to an environmental factor (e.g. climatic cooling) at these two levels. In the microevolutionary case, individuals with thicker fur within a population of a mammal species might have a selective advantage when temperatures decline and enrich their genes in the gene pool relative to competitors with a less thick fur, which

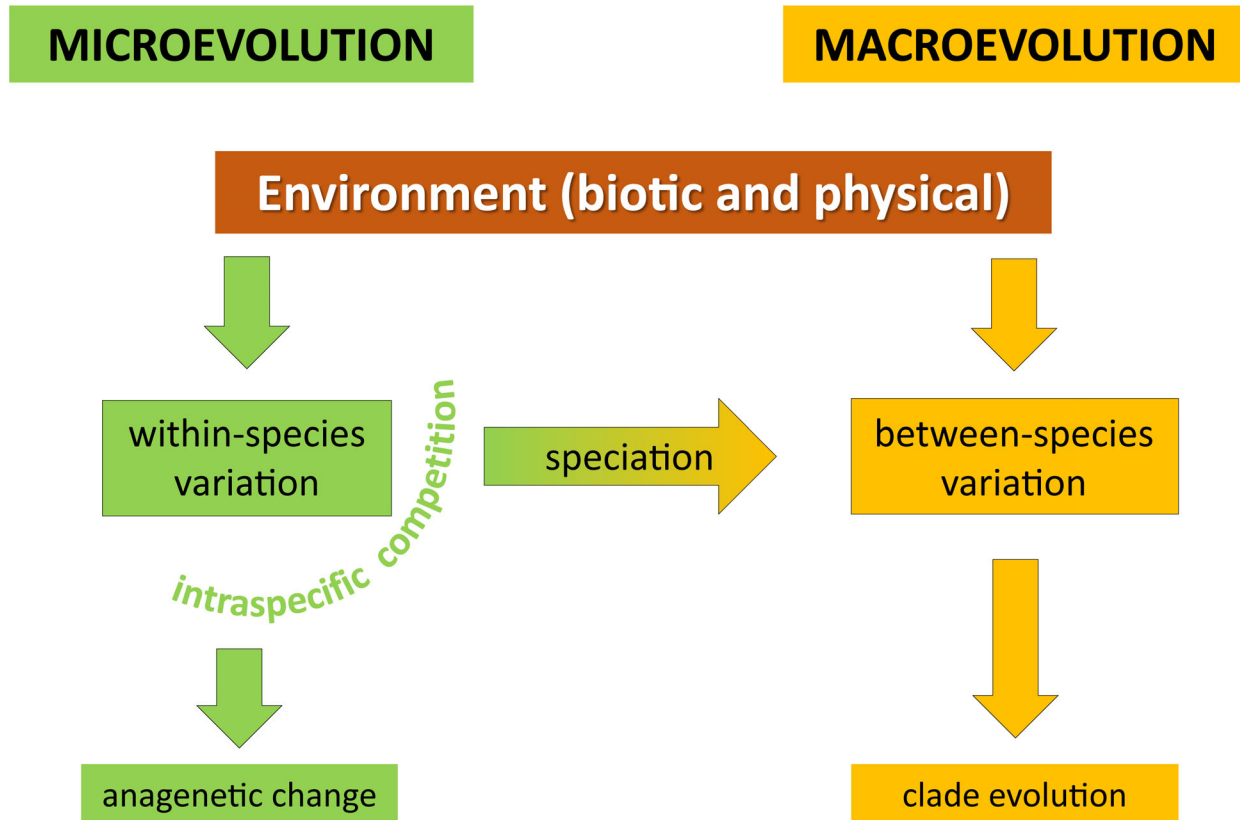


FIG. 2. Summary chart illustrating how microevolution and macroevolution combine to produce biodiversity and evolutionary change. Colour online.

leads to evolutionary change. Here, intraspecific competition mediated between selective agent and evolutionary response. On the macroevolutionary level, cooling might similarly help a mammal species with thick fur to out-compete a species with less thick fur, apparently analogously to the microevolutionary case. In contrast to microevolution, however, a mediating role of competition is not necessarily involved in macroevolutionary change. Cooling can increase the number of species with thick fur within a clade even in complete absence of interspecific competition, solely by driving less well-adapted species to extinction. The reason for this microevolutionary difference lies in the fact that sexual reproduction has no equivalent in macroevolution, which constitutes a principal difference in how evolution works at these two levels. In microevolution, the units of selection (organisms) are allied by gene pools and gene flow, whereas species in a clade are inert entities that only share common ancestry (cases of hybridization or lateral gene transfer might represent a third, somehow intermediate situation that is not treated herein). Accordingly, macroevolutionary success of a species with an advantageous trait is not laterally transferred within its clade (in absence of an analogue of

TABLE 1. Roles of intraspecific and interspecific competition in microevolution and macroevolution.

	Microevolution	Macroevolution
Intraspecific competition	Mediates all other agents of selection; weak driver of evolutionary change without this mediating role	—
Interspecific competition	Major driver of morphological divergence	Underlies positive correlation between speciation and extinction rates

a gene pool) and is therefore not inherently negative for the success of other species within the clade, unless these are direct competitors (see below). This case highlights the fact that evolutionary processes in microevolution and macroevolution are not completely analogous, and demonstrates that a clear conceptual definition of the fields facilitates the recognition of such differences.

Interspecific competition in macroevolution: data and theoretical conclusions

Although interspecific competition as a selective agent operates in macroevolution in the same way as any other selective agents by directly affecting (or not affecting) the existences of species, its macroevolutionary role might be more pervasive than that of most other factors. This conclusion is indicated by the observation that origination and extinction rates are usually positively correlated in a given clade. Recently, Marshall (2017) called this empirical rule ‘the third law of palaeobiology’ but I suggest the term ‘Stanley’s rule’ in recognition of the work of Steven Stanley, who was the first to address this phenomenon in detail (Stanley 1979, 1985, 1990). Stanley’s rule is probably the most general macroevolutionary rule; it is therefore surprising that it found relatively little interest in the subsequent literature. Stanley (1990) attributed the positive correlation between origination and extinction rates to five ecological factors: behavioural complexity, niche breadth, population size and stability, dispersal ability and habitat fragmentation. Each of these factors is certainly relevant, but I suggest here that Stanley’s rule is primarily a macroevolutionary aspect of van Valen’s (1973) Red Queen hypothesis (RQH).

Van Valen (1973) derived his RQH from two observations: (1) the probability of extinction of a taxon is constant and independent of its age (the ‘law of extinction’); (2) the probability of extinction is strongly related to adaptive zones, because different taxa have different probabilities of extinction. In other words, extinction occurs randomly with respect to age but nonrandomly with respect to ecology. Collectively, these two observations suggest that the effective environment of any homogeneous group of organisms deteriorates at a stochastically constant rate. Van Valen (1973) proposed that this is the result of an evolutionary zero-sum game driven by interspecific competition: the evolutionary progress (= increase in fitness) of one species deteriorates the fitness of coexisting species, but because coexisting species evolve as well, no one species gains a long-term increase in fitness, and the overall fitness of the system remains constant.

The name of the RQH refers to Lewis Carroll’s book *Through the Looking-Glass*, in which the Red Queen (a representation of a chess piece) says: ‘It takes all the running you can do, to keep in the same place.’ The metaphorical name implies permanently ongoing change, which was probably intended by van Valen (1973), but this connotation is unfortunate. As Vermeij & Roopnarine (2013, p. 563) stated, the RQH provides a microevolutionary explanation (continuous adaptive evolution within species) for a macroevolutionary phenomenon (constant extinction risk of taxa within a clade). Going one step further, it can be argued that the taxonomic survivorship curves (van Valen

1973, figs 1–7), which are the empirical basis for the ‘law of extinction’, are reflections of stasis rather than of permanent change within taxa, because the extended existence time of fossil taxa implies constant morphologies. (Morphology is the basis for the identification of fossil taxa, and an extended time of existence of a taxon can only be inferred if its morphology remains stable over this time.) Thus, ironically, the empirical basis of the RQH hypothesis holds only under the evolutionary regime of punctuated equilibria (PE), where morphological change is concentrated in speciation events (Eldredge & Gould 1972).

Fortunately, recasting the RQH in the framework of PE is conceptually unproblematic, because it is irrelevant in the RQH whether the evolutionary increase in fitness occurs continuously or during speciation events. In a PE context, the RQH simply implies that each speciation event in a clade deteriorates the fitness of coexisting species, which predicts a positive correlation between the rates of speciation and extinction in this clade (i.e. Stanley’s rule). Eventually, this argument from the RQH goes back to Darwin’s (1859) notion that closely related species compete most intensely, or, more generally, that members of a clade are on average stronger competitors than phylogenetically more distant species (niche conservatism; see Pyron *et al.* 2015 for a recent review). Research interest in the RQH has revived in recent years, with a lively debate between critics (e.g. Finnegan *et al.* 2008; Vermeij & Roopnarine 2013) and supporters (e.g. Quental & Marshall 2013; Žliobaitė *et al.* 2017). The match of RQH predictions with Stanley’s rule adds an argument in support of the RQH to this debate.

It should be noted that Stanley (1979, p. 229, 270) rejected the possibility that the correlation between origination and extinction rates results from niche crowding, which enables speciation only after extinction has made niche space available. His reservation against a niche crowding explanation stems from the fact that his data for rates of diversity increase (a surrogate for speciation in that work) in the discussed taxa were taken from geologic times of rapid diversification, where availability of niche space was apparently not a limiting factor. Although cause-and-effect is opposite in the niche crowding explanation (where extinction makes room for speciation) and in the Red Queen explanation (where speciation is a cause of extinction), the underlying control in both models is interspecific competition, which either prevents speciation or causes extinction. Does this mean that Stanley’s (1979) argument also casts doubt on the Red Queen explanation advocated herein? I think that there is a relevant difference, which results from the reversed cause-and-effect relationship of speciation and extinction in the two explanations. Stanley’s (1979) argument holds for questioning a niche crowding explanation, but in a Red Queen explanation where speciation causes

extinction, niche conservatism becomes an additional and critical factor. Niche space might have been largely empty during the episodes of rapid diversification that Stanley (1979) analysed, but if daughter species are as a rule ecologically very similar to their parent species, then competition between them remains a relevant factor even if more distant niche space is still unoccupied.

A second note concerns the question of how the intensity of interspecific competition affects the correlation between speciation and extinction. It might be predicted alternatively that the correlation breaks down if interspecific competition is very low, or that low interspecific competition correlates with low speciation and extinction rates and high interspecific competition with high rates. Available data support the second hypothesis, because Stanley's rule holds for taxa that are characterized by very weak interspecific competition (such as bivalves) and these have systematically lower rates of speciation and extinction than taxa with generally high intensity of interspecific competition (e.g. ammonoids and mammals; Stanley 1973, 1975, 2008).

CONCLUSIONS

Macroevolution is understood herein to be evolutionary change that is guided by sorting of interspecific variation. As such, macroevolution constitutes one of at least two levels at which evolution operates, and it combines with sorting of intraspecific variation (microevolution) to produce evolutionary change and biodiversity (Fig. 2). A general lesson from this concept is that the evolutionary role of selective agents can only be understood by analysing their effects on intraspecific and interspecific variation separately, which is a frequently neglected aspect in the study of potential drivers of evolutionary change. In addition, the herein advocated conceptual distinction between macroevolution and microevolution implies a number of specific conclusions:

1. The *process* of speciation in the sense of evolutionary change is microevolutionary, but the *outcome* (interspecific variation) and the *rate* of speciation are macroevolutionary.
2. Microevolution requires intraspecific competition as a mediator between selective agents and evolutionary response.
3. This mediating role of intraspecific competition is a unique feature of microevolution, which occurs only in the presence of sexual reproduction and the corresponding struggle for representation in the gene pool of the following generations.
4. Interspecific competition is a key process in macroevolution that predicts a prevalently positive correlation between origination and extinction rates (Stanley's rule).

Macroevolution as understood herein does not produce evolutionary novelties, but it determines their proliferation within the clades in which they evolved, and it adds species-level traits as non-organismic factors of sorting to this process. In this way, macroevolution eventually determines the fate of microevolutionary change.

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