What is punctuated equilibrium? What is macroevolution? A response to Pennell *et al.*

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What is punctuated equilibrium [or 'equilibria' as termed by one of us (N.E.)]? What is macroevolution? These are questions central to evolutionary biology. Yet, recently in an article in *Trends Ecol. Evol.* by Pennell *et al.* [1] the former is mischaracterized and the latter is not even defined. Here, we rectify these oversights by providing a definition of macroevolution, an accurate rendition of punctuated equilibrium (PE), and an elucidation of how they must be related. Furthermore, consider the title of [1]: 'Is there room for punctuated equilibrium...?' Such a question is flawed: concepts do not battle for *lebensraum*, although sometimes their opponents and proponents seem compelled to.

Macroevolution defined

We define macroevolution as: 'the patterns and processes pertaining to the birth, death, and persistence of species'. Simpsonian definitions of macroevolution considered it evolution above the species level. However, with such a definition, either macroevolution becomes meaningless, because there is no evolutionary process operating above the species level (i.e., no 'generification') or macroevolution is simply the study of pattern. By failing to define macroevolution, Pennell *et al.* fail to frame the scope of the problem they are considering.

What PE really is

We focus on three additional flaws in [1]. Two involve failure to define PE accurately and distinguish between the pattern of PE and the process(es) that produce it. The third is that Pennell *et al.* claim implications of the theory that are not correct. They admit they are not trying to find 'the true 'essence' of PE' ([1] p. 24), but this limits the validity of their conclusions, by allowing them to define PE any way they wish. They do so in a manner inconsistent with usage by the original framers of PE, and by numerous other subsequent authors. Pennell *et al.* ([1] p. 24) ascribe four research questions to PE: '(i) what is the relative importance of gradualistic versus pulsed evolution? (ii) what is the role of speciational events (cladogenesis) versus within lineage evolution (anagenesis) in generating trait divergence? (iii) when change is cladogenetic, are the changes adaptive or driven by neutral processes? and (iv) how important is higher-level selection (species selection) in shaping patterns of diversity?' Compare these with what PE actually states: species are stable (show stasis) throughout much of their evolutionary history; new species evolve cladogenetically when a daughter population become geographically isolated from its parent species (via allopatric speciation); PE entails implicitly that both the ancestral species and daughter species coexist for at least some time after the speciation event [2–5]. These are the patterns predicted by PE (and given the definition of macroevolution provided above, they suggest a crucial link between PE and macroevolution). Certainly, as part of PE, allopatric speciation is invoked. However, many different processes can act when a population becomes geographically isolated, running the gamut from selection to drift to neutral evolution, and so on; thus, many different processes can produce the pattern of cladogenesis in allopatry required by PE. Furthermore, let us consider the pattern of stasis. Again, many different processes can act to produce stasis in a lineage [4–6].

Given these statements about the actual, original, and subsequently generally used and intended meanings of PE, let us first return to three of the four points ascribed to PE in [1]. Points (i) and (ii) are statements about pattern and are not two distinct statements but instead intimately related ones. Gradualistic evolution necessitates anagenetic change. Pulsed evolution implies cladogenetic change except when an entire species transforms *en masse* into another species. Even if speciation ever happens this way, it is not a model of speciation consistent with allopatric speciation invoked by PE. Therefore, point (i) presented in [1] is a pattern that can be ascribed to PE. However, point (ii) is not entirely accurate because it either is synonymous with (i) or conflates the mechanism of speciation invoked by PE. How does Pennell *et al.*'s point (iii) fare? PE states that speciation occurs allopatrically, but many different processes can transpire in allopatry to cause population divergence. Therefore, point (iii) of [1] is a statement about processes of allopatric speciation, demonstrating the notion that Pennell *et al.* conflate pattern with process in their consideration of PE. To the extent that Mayr [7], the source for Eldredge and Gould's mechanism of speciation [2], invoked nonadaptive factors, we can suppose that PE included the possibility of these, but it is never explicitly stated as a requirement of PE (e.g., [2–5]). Certainly, Gould and others [5,8] argued that adaptation need not be invoked to explain every episode of diversification. However, most of these discussions were not in the context of PE, but were part of discussions in the adaptive radiations literature. Nowhere was it suggested in [2] or in any paper

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by Eldredge or Gould authored together or separately on PE (or in many other subsequent papers that considered PE; e.g., [6,9]) that, for PE to be validated, speciation events must involve nonadaptive factors. Thus, point (iii) of [1] conflates the pattern and the process of PE and is an erroneous extrapolation of its implications.

Species selection is not required by PE

Finally, we turn to Pennell *et al.*'s point (iv), which focused on the importance of species selection. The authors argued that, for PE to hold, species selection must be an important evolutionary force. However, as they acknowledge, species selection has long been a controversial topic. In fact, let us consider their definition ([1] p. 29]) of species selection. They acknowledge that it 'ignore(s)' the distinction between species selection and sorting made by Vrba and Gould! [10]. Indeed, the definition of species selection that Pennell *et al.* use does not match the definition of species selection used in many publications, including those authored or coauthored by the architects of PE [4,10,11]. Indeed, various authors have argued that species selection is unlikely to have a major role in evolution [4,10,11], yet these authors endorsed PE. It is true that, in some publications (e.g., [5]), Gould used a definition of species selection corresponding to that used by Pennell *et al.* [1], but he waffled on this issue [5,11]. Furthermore, he never stated that, for PE to be validated, species selection must occur. (Gould [5] argued that documenting species selection was important for the independence of macroevolutionary theory.) In addition, it is clear from papers authored or coauthored by the architects of PE that species selection never had to be a prominent evolutionary force for PE to prevail. Indeed, the only source that we could find for this was [1]. By contrast, Eldredge and Gould [2] stated that, with PE, explaining trends required differential generation and survival of species; Stanley [12] referred to this pattern as species selection. Contra [12], various authors [4,9–11] have argued that this pattern should be called 'species sorting', which can sometimes involve the process of species selection. In any case, differential survival and generation of species remains a pattern entailed by PE, but species selection is not entailed. Therefore, Pennell *et al.*'s point (iv) does not deal directly with PE; failure to document species selection does not refute PE.

In summation, it is not PE that conflates four separate primary research questions, but Pennell *et al.*'s interpretation and extrapolation of PE that does. Still, we agree that a 'truly synthetic macroevolutionary research program will involve the melding of data and theory from different disciplines' ([1] p. 30) and is desirable.

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