TITLE: Metabolic rates, climate and macroevolution: A case study using Neogene molluscs

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Keywords: extinction, body size, temperature, bivalve, gastropod, hierarchy

ABSTRACT

Basal metabolic rate is posited to be a fundamental control on the structure and dynamics of ecological networks, influencing organism resource use and rates of senescence. Differences in the maintenance energy requirements of individual species therefore potentially predict extinction likelihood. If validated, this would comprise an important link between organismic ecology and macroevolutionary dynamics. To test this hypothesis, the basal metabolic rates of organisms within fossil species were determined using body size and temperature data, and considered in light of species' survival and extinction through time. Our analysis focused on the high-resolution record of Pliocene to recent molluscs (bivalves and gastropods) from the Western Atlantic. Species-specific basal metabolic rates were calculated by measuring the size range of specimens from museum collections, determining ocean temperature using the HadCM3 global climate model, and deriving values based on relevant equations. Intriguingly, a statistically significant difference in metabolic rate exists between those bivalve and gastropod taxa that went extinct and those that survived throughout the course of the Neogene. This indicates that there is a scaling up from organismic properties to species survival for these communities. Metabolic rate could therefore represent an important metric for predicting future extinction patterns, with changes in global climate potentially affecting the lifespan of individuals, ultimately leading to the extinction of the species they are contained within. We also find that, at the assemblage level, there are no significant differences in metabolic rates for different time intervals throughout the entire study period. This may suggest that Neogene mollusc communities have remained energetically stable, despite many extinctions.

1. INTRODUCTION

Metabolic rate is defined as the rate of energy uptake, transformation, and allocation for an individual organism [1], and plays a fundamental role in resource use and rates of senescence [1-5]. Notably, population dynamics [6], geographic patterns in species richness [7], and community dynamics [8] are all related to body size and temperature, the primary determinants of metabolic rate for poikilotherms. There is also an association between metabolic rate and latitudinal diversity gradients, and perhaps between metabolism and rates of speciation [1, 7, 9]. These examples provide a clear connection as to how ecological processes operating at the organismic level scale up to higher level patterns, a hypothesis previously investigated in a variety of modern [1, 7, 10, 11] and fossil ecosystems [12-14]. Here, we explore the relationship between metabolic rate and extinction to try to further consider the connection between organismic ecology and macroevolutionary dynamics [15-18]. As metabolic rate is a primary control for traits important for identifying extinction likelihood [19] and with maximum life span shown to scale with body size and temperature [4, 20, 21], we propose metabolic rate itself as a potential proxy for identifying the extinction probability of a species. Specifically, we would expect that species with higher mean metabolic rates are more likely to go extinct than species from the same clade with lower mean metabolic rates.

The dataset we use to assess this possibility is the Pliocene (5.333 Mya) to recent molluscan fauna of the Western Atlantic, a region that has experienced significant fluctuations in climate and ambient temperatures [22-26]; perturbations that have been previously linked to species turnover [27, 28]. The diverse, well preserved and abundant molluscan fauna of this region has been frequently used to study macroevolution in the fossil record [17, 29-31]. Utilising both extant and fossil species provides a pool of confirmed extinct species whose metabolic rates can be compared with those of coeval still extant species.

Our analysis focuses on basal metabolic rate (BMR), representative of the maintenance energy requirements of an individual organism. For modern taxa, the BMR of animals can be determined through direct measurement of resting respiration rate. This is not possible for fossil organisms, so instead we employ an energetic model based on the allometric scaling of energy requirements with body size to estimate BMR [32]. This method has been successfully applied in previous paleontological studies (e.g. [12-14]). In this model, BMR is related to body size, temperature and clade specific characteristics (equation presented below), all parameters that can be readily determined for fossil (and extant) organisms.

For 299 species of North American bivalves and gastropods, we calculate BMR by combining measures of body size with detailed estimates of ocean temperature sourced from the HadCM3 global climate model [33, 34]. One hundred and seventy-eight of these species became extinct during the study interval. Identifying if a difference in BMR exists between these two species pools offers a potential metric for predicting future extinction patterns as well as a means of considering other extinction intervals in the fossil record. Further, tabulating what changes occur in BMR at the assemblage level across the study time interval, when considered in light of theoretical approaches to community ecology, may enhance our understanding of extinction as both an ecological and genealogical phenomenon [16, 18, 35].

2. RESULTS

A full description of all methods used to generate the results below is provided in the electronic supplementary material.

(a) BMR AS A PREDICTOR OF EXTINCTION LIKELIHOOD

Using the total dataset (Supplementary Table 1), for both bivalves and gastropods, we find a significant difference in $B_{species}$ between extinct and extant species (Mann-Whitney $P < 0.0005$ for both bivalves and gastropods) with medium effect sizes for both clades (Supplementary Table 5). BMR values are higher for extinct species (Figure 1).

Varying the ambient palaeo-temperature, removing temperature entirely from the calculation, removing the scaling constants, and removing outliers in the size distribution does not change either the direction nor significance of these results, although there is almost always a reduced effect size (Supplementary Table 5). When we randomly designate species as either extinct or extant in equal proportions, we are only able to obtain a significant difference in BMR values between the extinct and extant categories (Mann-Whitney $P < 0.05$) 1.6 % of the time with bivalve datasets and 1.45 % of the time with gastropod datasets (out of 10,000 replicates total, 160 and 145 times for bivalves and gastropods, respectively). Potential differences in BMR between families do not seem to impinge upon our overall result. Neither extinct nor extant species are confined to a specific group of families, many families contain both extinct and extant species and our statistical tests for such a possibility do not support substantial variation in BMR among families. For bivalves, pairwise comparisons of families (using $B_{species}$ and corrected for multiple comparisons) produce a significant difference in only 1 out of 171 comparisons; for gastropods, they produce a significant difference in only 8 out of 325 comparisons. Moreover, for both clades, the pairwise comparisons that yield significant results include both extinct and extant species. Finally, as there is a lack of correlation between $B_{species}$ and latitude (Supplementary Figure 1), our result does not seem to be primarily due to differences in latitude between extinct and extant species.

With the results of sensitivity tests consistent with those obtained for the total data set, the low percentage of significant results for datasets with random status assignment, negligible statistical difference in BMR among families, and no apparent association between latitude and BMR, this suggests that the difference in BMR values between extinct and extant species is unlikely to be an artefact of our choice of input parameters, statistical power issues, taxonomy, or the latitudinal temperature gradient. We therefore consider our original supposition, that the representative metabolic rate of a species is a predictor of extinction likelihood, to be upheld.

(b) BMR AS A PREDICTOR OF EXTINCTION LIKELIHOOD, PARTITIONED BY BROADLY VERSUS NARROWLY DISTRIBUTED SPECIES

Considering those species in our dataset identified as broadly distributed (our potential generalist species) versus the remainder of the fauna, we find that for the broadly distributed species there is no significant difference in BMR between extinct and extant species for bivalves (Mann-Whitney $P = 0.137$) or gastropods (Mann-Whitney $P = 0.085$) (Figure 1). By contrast, for the narrowly distributed species, the significant difference retrieved for all species is maintained (Both clades Mann-Whitney $P < 0.003$; Figure 1). Adjusting our input parameters as described above for our sensitivity analyses results in the same outcome for bivalves and in the majority of cases for gastropods (Supplementary Table 5). Thus, the signal retrieved in the analysis of the entire dataset is primarily derived from patterns among the narrowly distributed species. Whilst broadly distributed taxa come from only a small selection of taxonomic families (Supplementary Table 1), the families that contain broadly distributed species also contain narrowly distributed species. When the clade specific scaling constant is removed from our BMR calculation, the difference in the patterns identified for broadly versus narrowly distributed species remains unchanged for bivalves, but does change for broadly distributed gastropod species (Supplementary Table 5). It may be the case that the difference in result for broadly versus narrowly distributed taxa reflects differences in metabolism among higher order clades, but further exploration of this result, likely best achieved using phylogenetic methods, is necessary to confirm this.

(c) CHANGES IN BMR AT THE ASSEMBLAGE LEVEL

For both bivalves and gastropods, we find no difference in the distribution of assemblage level metabolic rates for each of our Neogene time bins (Kruskal-Wallis P > = 0.4; Figure 2). These results were resilient to the various sensitivity analyses (all p-values > 0.3) and are manifest in spite of significant changes in diversity across the study period (Supplementary Figure 2; Supplementary Table 7). This result indicates that western Atlantic mollusc assemblages within formations have been energetically stable throughout the late Neogene, even in the face of numerous extinctions and climatic changes.

3. DISCUSSION

By assessing macroevolutionary patterns of Neogene molluscs from the western Atlantic in the context of palaeoclimatic models, we identify metabolic rate as playing a significant role in mediating extinction and survival (Figure 1). In particular, species with lower reconstructed BMR values are more likely to survive than their higher BMR molluscan kin. This result is resilient to a variety of sensitivity tests and thus cannot be attributed merely to uncertainties in key parameters used in our metabolic rate calculations or other possible sources of error. The results derived herein come from only a limited taxonomic sampling and restricted time period. However, if they are more broadly generalizable then this would suggest a possible connection between metabolism and the death of both individuals and species (see also [4, 21]), as previous studies have demonstrated that, for individual organisms, higher metabolic rates correlate with both higher mortality rates and higher rates of cell decay (e.g. [4, 36-39]). Metabolism may therefore represent an important control on mortality at multiple hierarchical levels *sensu* Vrba and Eldredge [40], Eldredge [16, 41], Lieberman et al. [18], Jablonski [17], Eldredge et al. [42], Tëmkin and Serrelli [43], and Fábregas-Tejeda and Vergara-Silva [35]. Moreover, it suggests that a direct continuum exists between an organism-level phenomenon (metabolic rate) and a species-level response (extinction) such that processes operating at a lower hierarchical level can be extrapolated to explain patterns produced at a higher hierarchical level.

Differences in metabolic rate between extinct and extant species reinforces established predictions of the Metabolic Theory of Ecology (or MTE; [1]), which champions metabolic rate as the fundamental control on macroecological processes and most observed patterns in ecology. Connecting metabolic rate to global biodiversity patterns via MTE has primarily focused on establishing that generation times of individuals and mutation rates (and ultimately speciation) have a Boltzmann relation to temperature (represented by ‘k’ in our BMR equation; [7, 11]). A metabolic explanation for extinction would place extinction at an equivalent level to speciation in an MTE framework, rather than being either a stochastic process [44] or only a function of speciation rate and population abundance [11].

However, our result does not imply that metabolic rate is the sole driver of extinction. For instance, the difference we observe between BMR of extinct and extant species may reflect variation in a constellation of organismic traits such as developmental rate, time to maturity, life span and population size, with a primary causal factor driving these differences being variation in the rate of energy uptake [1, 19, 45]. Further, there are other cases where population or species-level factors, or even shear chance, may be influencing patterns of extinction (see extensive discussions in [15-17, 19, 40, 41, 46-48] and references therein). The difference in result identified for broadly distributed versus narrowly distributed species also certainly advocates for a level of complexity in explaining extinction that extends beyond simple BMR values. Nevertheless, that a difference exists in BMR between extinct and extant species does demonstrate a metabolic component to extinction that was previously putative [4, 21].

At the macro-scale, the BMR for the Western Atlantic mollusc assemblage within any given time interval seems to show dramatic stasis over a substantial period of time and in the face of numerous extinctions (178 species), significant changes in diversity (Supplementary Figure 2; Supplementary Table 7) and major climate change [22-26]. The small number of time bins limits the broader significance of these results, but the lack of variability across the study period does intimate that Neogene mollusc assemblages have remained energetically stable (Figure 2). Previous work over a much longer time period identified stasis in per capita metabolic rate for Cenozoic gastropods [13], congruent with our result. An important caveat, however, is that the assemblages we have constructed do not strictly represent biological communities, given the resolution of the fossil record, but in general, this result seems to support the notion that ecosystems can at times best be defined as functional groups rather than being viewed in the context of the composition of particular taxa [49, 50].

Presuming that the maintenance of mean metabolic rate for Neogene mollusc communities is a genuine phenomenon, this is consistent with a qualified form of ecological stasis [51], where the energy budgets of populations remain unchanged over long periods of time despite changes in taxonomic membership, environmental change, extinction and species invasions. Mean per capita metabolic activity at the macroscale can remain stable if any potential decrease in metabolic activity, such as extinction of a species, is mitigated by an increase in diversity (with new species subject to energetic equivalence), increased abundance of one or more existing species (with a subsequent reduction in mean size) or through invasion by immigrant species. These three mechanisms are not mutually exclusive and any or all of them could explain the pattern we observe. This scenario parallels Eldredge's [52] 'sloshing bucket' theory, with the turnover in Neogene mollusc communities seemingly not enough to lead to extreme ecological disruption.

4. CONCLUSIONS

When it comes to species, we do find a significant difference between the BMRs of extinct and extant taxa. When we extend our analysis to an assessment of mean BMR at the assemblage level over time, even in the face of significant climate change, there are no significant differences among the macro-level assemblages from different time periods. Together, these findings suggest that under certain circumstances when it comes to extinction a continuum exists between phenomena at the level of the individual through to the level of a species, but that communities may be better defined as functional groups rather than by their species composition. Thus, understanding metabolic rate for fossil communities can provide crucial insight into extinction as an ecological and genealogical phenomenon (sensu [16, 42]).

ACKNOWLEDGEMENTS

We thank Roger Portell (FLMNH) for both providing images of specimens and for offering information on the geological context of the molluscan assemblages used in this study. We thank Stephen Hunter (University of Leeds) for providing paleoclimatic data. PaleoGIS and PaleoWeb are plate tectonics reconstruction and basin modeling software developed by The Rothwell Group, L.P and we thank them for providing this software for palaeo-coordinate reconstructions. We would also like to acknowledge all contributors to the Digital Atlas of Ancient Life and iDigBio (both those individuals responsible for setup, maintenance and administration and those who have contributed content) as both of the data repositories made this study possible. Two anonymous reviewers provided important feedback that improved the overall quality of our paper. LCS and BSL were supported by NSF grants # EF-1206757 and DBI-1602067.

ETHICS STATEMENT

This manuscript has not been published in whole or in part elsewhere and is not currently being considered for publication in another journal.

DATA ACCESSIBILITY STATEMENT

All additional data for this article is provided in Supplementary Tables 1-7

COMPETING INTERESTS STATEMENT

We declare we have no competing interests

AUTHORS' CONTRIBUTIONS STATEMENT

L.C.S and B.S.L. conceived the study. L.C.S and J.K. compiled mollusc data. E.E.S provided palaeoclimate data and reconstructed palaeo-coordinates for Pliocene occurrences. L.C.S. performed all analyses and drafted all figures. L.C.S and B.S.L. wrote the manuscript with input from all co-authors. All authors gave final approval for publication.

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FIGURE CAPTIONS

FIGURE 1

Distribution of $\log_e$BMR (in Watts) for extinct versus extant bivalves and gastropods based upon our total Neogene mollusc dataset, for only broadly distributed species and for only narrowly distributed species. Values for extant species in blue and extinct species in orange. Horizontal bars represent median values, boxes enclose the 25th through 75th percentiles, and whiskers indicate 1.5 x interquartile range.

FIGURE 2

Mean per capita $\log_e$BMR (in Watts) of Western Atlantic bivalves and gastropods for each of five separate time bins (early Pliocene, late Pliocene, early Pleistocene, middle Pleistocene, late Pleistocene) based upon results generated using Equation 2. Error bars represent standard error.