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Interactive effects of intrinsic and extrinsic factors on metabolic rate

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Metabolism energizes all biological processes, and its tempo may importantly influence the ecological success and evolutionary fitness of organisms. Therefore, understanding the broad variation in metabolic rate that exists across the living world is a fundamental challenge in biology. To further the development of a more reliable and holistic picture of the causes of this variation, we review several examples of how various intrinsic (biological) and extrinsic (environmental) factors (including body size, cell size, activity level, temperature, predation and other diverse genetic, cellular, morphological, physiological, behavioural and ecological influences) can interactively affect metabolic rate in synergistic or antagonistic ways. Most of the interactive effects that have been documented involve body size, temperature or both, but future research may reveal additional 'hub factors'. Our review highlights the complex, intimate inter-relationships between physiology and ecology, knowledge of which can shed light on various problems in both disciplines, including variation in physiological adaptations, life histories, ecological niches and various organism-environment interactions in ecosystems. We also discuss theoretical and practical implications of interactive effects on metabolic rate and provide suggestions for future research, including holistic system analyses at various hierarchical levels of organization that focus on interactive proximate (functional) and ultimate (evolutionary) causal networks.

This article is part of the theme issue 'The evolutionary significance of variation in metabolic rates'.

1. Introduction

Metabolism embodies the complex assembly of biochemical reactions that all organisms use to transform environmental resources into various structures and activities. Given that metabolism can only occur as a result of a dynamic interaction between the internal and external environments of an organism, it is not surprising that many kinds of intrinsic (biological) and extrinsic (external environmental) factors can affect its tempo [1–10]. Understanding what causes the broad variation in metabolic rate that exists in the living world is a fundamental challenge in biology because metabolic rate is an important indicator of the 'pace of life', which can significantly influence the ecological success and evolutionary fitness of organisms ([5,10–12]; but see [13,14]). After many decades of research, we now know much about the effects of many intrinsic and extrinsic factors, especially body size, activity level and temperature, on metabolic rate both within and among species [8,15–24]. However, most studies have examined the effects of each of these factors individually, irrespective of the effects of other factors. Although useful and necessary for causal analyses, single-factor analyses essentially assume that other factors not directly analysed have independent effects on metabolic rate. By contrast, multiple-factor analyses are increasingly showing that the effect of one factor on metabolic rate may depend on the effects of other factors. To obtain a realistic, more complete picture of how various factors affect metabolic rate, these interactive effects should be identified and quantified.

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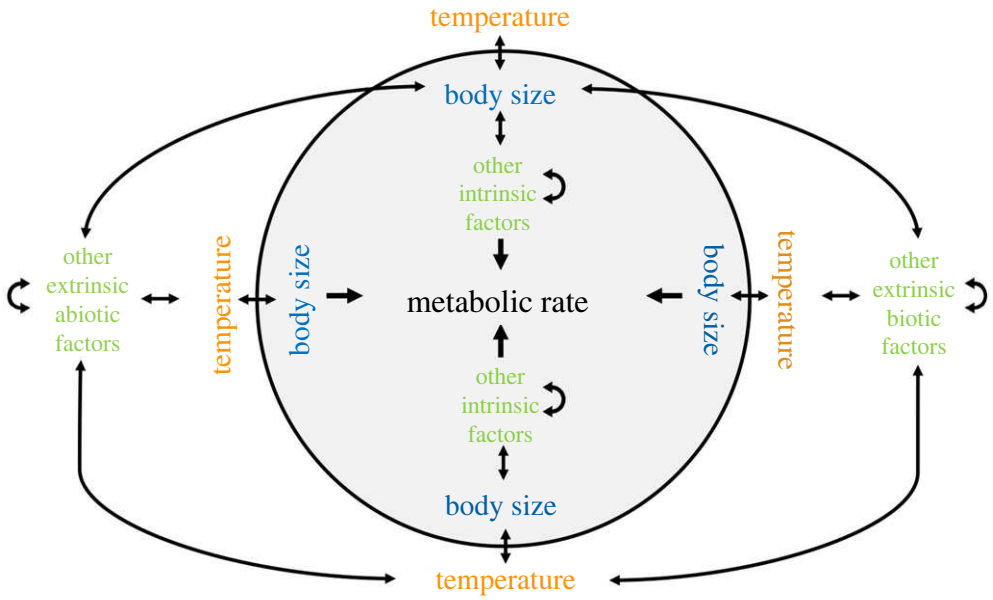

Figure 1. Schematic depiction of interactive effects of body size, temperature, and other intrinsic and extrinsic factors on metabolic rate. Body size and temperature are pictured prominently because not only are they the most influential intrinsic and extrinsic factors, respectively, but also these factors are most often involved in multifactorial interactive effects. Other intrinsic factors include genotype, sex, body shape and composition, activity level, developmental stage, thermoregulatory mode, reproductive state and rate and cellular mode of growth. Other extrinsic abiotic factors include salinity, acidity (CO_2 levels), oxygen supply, water availability, light intensity, season, captivity and habitat. Other extrinsic biotic factors include food organisms, predators and parasites. More details are provided in the text and table 1.

Furthermore, an understanding of interactive effects on metabolic rate has major theoretical and practical implications (also see §6). For example, the influential 'metabolic theory of ecology' (MTE) assumes that body size and temperature have independent multiplicative effects on metabolic rate, and that the mass-scaling exponent for metabolic rate is fixed at 3/4 [18]. However, as will be seen, these factors can interactively affect metabolic rate in synergistic or antagonistic ways, and these interactions should be incorporated into theoretical models to improve their predictive accuracy. In addition, many comparative studies of the effects of various environmental factors on metabolic rate have assumed that they act independently of the effect of body size. Based on this assumption, the effect of body size is 'removed' by analysis of covariance and other statistical methods that assume no interaction between the effects of body size and the environmental factor being considered. However, interactive effects complicate these attempts at 'body-size correction' [25].

Diverse intrinsic and extrinsic factors significantly affect metabolic rate both in relation to and independently of body size. Recognition of these systematic, repeatable effects has convinced many biologists that the mass-scaling exponent for metabolic rate is highly malleable (as a result of interactive effects of body size and other factors on metabolic rate), thus undermining the once widely accepted 3/4-power law of metabolic scaling [9]. Although the MTE is correct in highlighting the substantial effects that body size and temperature have on metabolic rate [8,15,26,27], we show that our understanding of variation in the rates of metabolism and other associated biological and ecological processes will remain incomplete and even misleading until the interactive effects of body size, temperature, and numerous other intrinsic and extrinsic factors become better known and appreciated (figure 1).

Therefore, two major purposes of this review article are to (i) discuss how various intrinsic and extrinsic factors can interactively cause or be associated with variation in metabolic rate both within and across species (schematically represented in figures 1 and 2; and details with literature sources provided in table 1), and (ii) show why these interactive effects should be considered in theoretical models or methodological approaches focused on the rates and (or) size dependencies of metabolism and other biological and ecological processes and patterns that depend on metabolic energy, such as rates of growth, development, and reproduction at the individual level, and size-abundance relationships at the population and community levels. We conclude that a holistic system view of metabolic rate, involving interactive multi-directional functional and evolutionary causal networks, is much needed.

2. Interactive effects of intrinsic factors

Body mass is the most important intrinsic factor affecting metabolic rate. Indeed, the rate of metabolism (R) has often been well described by the power function $R = aM^b$, where a is the scaling coefficient (or antilog of the intercept in a log-linear plot), M is body mass, and b is the scaling exponent (slope in a log-linear plot) [238,239]. Therefore, most interactive effects between intrinsic factors on metabolic rate involve body mass. They include significant effects of taxonomic affinity, cell size (including cellular mode of growth), genome size, genotype, gender (sex), activity level, mode of locomotion, mode of thermoregulation, growth rate, life-history stage, body shape, food processing (specific dynamic action), reproductive state, reproductive strategy, molt-cycle phase, body composition and social behaviour on the body-mass scaling exponent (b) for metabolic rate (see table 1). Other interactive effects of intrinsic factors on metabolic rate include colony size and connectedness [117], gender and reproductive effort [118] and trinary interactions among body size, genotype and life-history stage [43].

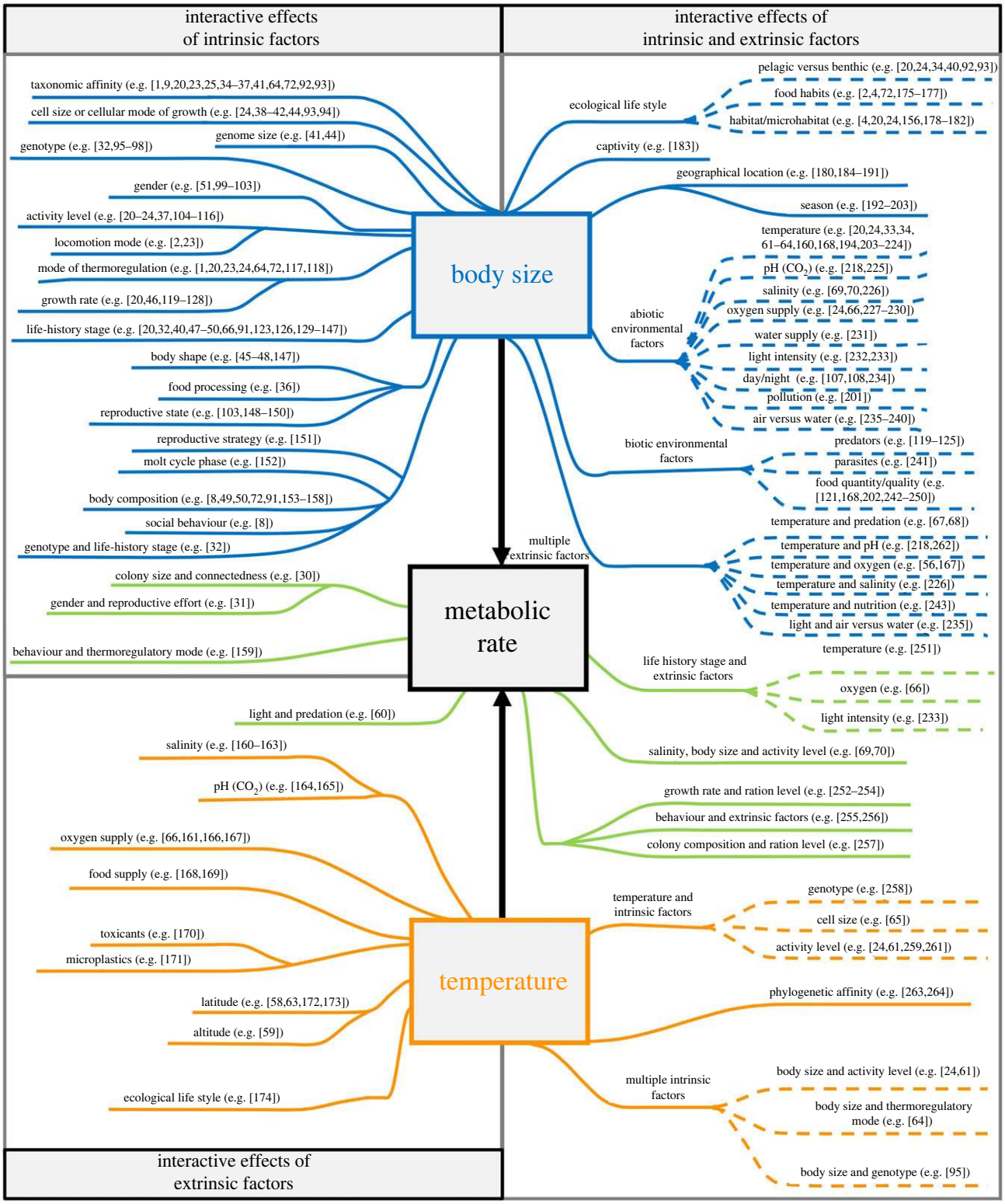

Figure 2. Examples of various types of interactive effects between intrinsic factors, extrinsic factors, and both on metabolic rate (documented by indicated references: for more details, also table 1). Interactive effects involving body mass and other intrinsic and extrinsic factors are represented by blue lines. Interactive effects involving temperature and other intrinsic and extrinsic factors are represented by red lines. Other joint effects of intrinsic and extrinsic factors on metabolic rate are indicated by purple lines. Dashed lines designate multiple examples of a specific class of interactive effects.

Hypothetical mechanisms underlying many of the various interactive effects of body size and other intrinsic factors on metabolic rate are described in table 1. The most important mechanisms appear to involve (i) geometric constraints on resource supply and metabolic waste removal, as related to surface area (SA) to volume (V) ratios at both the cellular and organismal levels, (ii) effects of various resource-demanding processes on metabolic rate, and (iii) the relative proportions of the body that consist of tissues with high versus low metabolic rates. These effects can be viewed in the context of two interrelated theoretical frameworks, the 'metabolic-level boundaries hypothesis' (MLBH) [23,24] and the 'contextual multimodal theory' (CMT) of metabolic scaling [8,27].

According to the MLBH, how metabolic rate (R) relates to body mass (M) (i.e. its scaling exponent b) depends on the

Table 1. Examples of various types of interactive effects between intrinsic factors, extrinsic factors, and both on metabolic rate, with brief descriptions of the direction of each effect and hypothetical mechanism(s), if known.

interactive effects of intrinsic factors			
type	direction of interactive effect[a]	underlying mechanism	selected sources
body size and taxonomic affinity	variable	related to differences in physiological/ecological lifestyle that are described below	[1,9,20,23,25,28–36]
body size and cell size or cellular mode of growth	variable	mass-scaling of metabolism depends on cell size and the cellular mode of growth (i.e. cell enlargement versus multiplication, which affects metabolically relevant cellular surface area to body volume ratios)	[24,32,36–42]
body size and genome size	variable	mass-scaling of metabolism relates to genome size, presumably because of its association with cell size (see above)	[32,41]
body size and genotype	variable	mass-scaling of metabolism differs between genotypes for unknown reasons	[43–47]
body size and gender size	variable	mass-scaling of metabolism differs between males and females often for unknown reasons. Gender-related differences in body composition may be involved in some cases (e.g. in humans where gender differences in metabolic scaling disappear when fat-free body mass is considered)	[48–53]
body size and activity level	positive or negative	mass-scaling of metabolism varies with activity level, according to shifts in the relative Importance of surface-area versus volume related metabolic processes (following the metabolic-level boundaries hypothesis', MLBH [23,24]. Mass-scaling exponents (slopes) tend to increase (approaching 1) with upward shifts from resting (basal) to active metabolism, or downward shifts from resting to torpid metabolism	[20–24,31,54–66]
body size and mode of locomotion	negative or positive effect of flying ability	winged insects show shallower mass-scaling of metabolic rate than do wingless insects. By contrast, volant mammals (bats) show steeper metabolic scaling than do small terrestrial mammals (e.g. shrews and rodents). In both cases, the mass-scaling exponent is inversely related to the overall metabolic level, as predicted by the MLBH	[2,23]
body size and mode of thermoregulation	negative (ectothermy to endothermy)	endothermic animals tend to show shallower mass-scaling of metabolism than do ectothermic animals, presumably because surface-area related heat loss and thermal conductance play more of a role in the metabolic scaling of endotherms that maintain a constant body temperature than for that of ectotherms with variable body temperatures. The mass-scaling exponent is inversely related to metabolic level, as predicted by the MLBH	[1,20,23,24,33,34,67,68]
body size and growth rate	positive	ontogenetic mass-scaling exponents for metabolism tend to correlate positively with the rate of growth, which is a volume-related process (i.e. the slope tends to approach 1)	[20,69–79]
body size and life-history stage	usually negative (early to late ontogeny)	ontogenetic mass-scaling exponents for metabolism often shift significantly across developmental (life-history) stages because of changes in growth rate, cellular mode of growth, mode of thermoregulation, level or mode of activity, and (or) body shape/composition	[20,39,43,74,77,80–104]
body size and body shape	positive for shape flattening or elongation	intraspecific mass-scaling of metabolism in organisms that use cutaneous respiration relates to ontogenetic shifts in body shape, and thus surface area to volume ratios	[69,80,81,104,105]
body size and food processing	positive	food processing (specific dynamic action) increases the mass-scaling exponent for metabolic rate	[30]

(*Continued*.)

Table 1. (*Continued.*)

interactive effects of intrinsic factors			
type	**direction of interactive effect[a]**	**underlying mechanism**	**selected sources**
body size and reproductive state	variable	ontogenetic mass-scaling exponents for metabolism may be altered by metabolic requirements for reproduction, including eggs	[53,106–108]
body size and reproductive strategy	negative	in eutherian mammals, the mass-scaling of metabolic rate is steeper in species with litter sizes = 1, than those with litter sizes > 1	[109]
body size and molt cycle phase	variable	the mass-scaling exponent for metabolic rate varies with molt cycle phase in a snake	[110]
body size and body composition	usually negative	intra- and inter-specific mass-scaling exponents for resting metabolism may depend on mass-related changes in body composition (e.g. decreases in relative masses of organs/tissues with high metabolic costs, including brain, heart, liver and kidneys, but increases in relative masses of metabolically inexpensive tissues, such as fat, connective, skeletal and resting muscle tissues)	[8,34,82,83,85,111–116]
body size and social behaviour	variable	huddling behaviour alters the mass-scaling of resting metabolic rate in small mammals because huddle surface area primarily determines heat loss and thus compensatory metabolic heat production, rather than individual surface area	[8]
body size, genotype and life-history stage	variable	ontogenetic shifts in the mass-scaling of metabolism vary with genotype in *Drosophila*, apparently owing to variable developmental timing in switching from anaerobic to aerobic ATP production	[43]
colony size and connectedness	negative	zoid connectedness increases metabolic rate more in small than larger ascidian colonies. The mass-scaling exponent is near 1 in unconnected colonies, but less than 1 (0.80) in connected colonies, possibly owing to interactive effects among the zooids	[117]
gender and reproductive effort	positive for females	reproductive effort increases metabolic rate in female, but not male snakes (*Tomodon dorsatus*), presumably because of the high energy cost of egg production	[118]
behaviour and thermoregulatory mode	stronger in ectotherms	relationships between metabolic rate and behavioural traits are generally stronger in ectotherms than endotherms	[119]
interactive effects of extrinsic factors			
type	**direction of interactive effect[a]**	**underlying mechanism**	**selected sources**
temperature and salinity	negative or complex	thermal response of metabolic rate decreases (or shows complex relationships) with increasing salinity. Higher temperature speeds up metabolism, whereas higher salinity reduces osmoregulatory metabolic demand in marine organisms. However, hypersaline conditions may increase metabolic costs in freshwater/estuarine organisms	[120–123]
temperature and pH (CO_2)	variable (species-specific)	combined effects of temperature and acidification (CO_2 levels) vary with species for unknown reasons	[124,125]

(*Continued.*)

Table 1. (*Continued.*)

interactive effects of extrinsic factors			
type	**direction of interactive effect[a]**	**underlying mechanism**	**selected sources**
temperature and oxygen supply	positive	thermal response of metabolic rate increases with increasing oxygen supply, perhaps because it can be expressed more freely when high-temperature causing hypoxia in water is prevented. However, temperature acclimation can mitigate effects of hypoxia on metabolic rate	[84,121,126,127]
temperature and food supply	complex	thermal sensitivity of metabolism varies with food supply in complex ways	[128,129]
temperature and toxicants	complex	thermal sensitivity of metabolic rate in a moth depended on an insecticide treatment when acclimated at 22°C, but not when acclimated at 28°C	[130]
temperature and microplastics	complex	in an aquatic amphipod, temperature effects are positive at low microplastic concentration, but negative at high microplastic concentration, for unknown reasons	[131]
temperature and latitude	positive (low to high latitude)	high-latitude populations in relatively cool habitats tend to show more thermal sensitivity of metabolic rate than that of low latitude populations in warmer habitats	[132–135]
temperature and altitude	positive (low to high altitude)	a high-altitude population of the tsetse fly *Glossina pallidipes* in a cool habitat showed higher temperature sensitivity of metabolic rate than did low-altitude populations in warmer habitats	[136]
temperature and ecological life style	complex	invasive crayfish show higher metabolic rates at warm temperatures, but lower metabolic rates at cooler temperatures than do native crayfish	[137]
light and predator cues	positive or negative	metabolic rate of an aquatic amphipod changes in response to fish predator cues in light, but not in dark	[138]

interactive effects of intrinsic and extrinsic factors			
type	**direction of interactive effect[a]**	**underlying mechanism**	**selected sources**
body size and ecological life style			
pelagic versus benthic	positive or negative (comparing pelagic species to benthic species)	pelagic invertebrate/protist species (or life-stages) tend to show steeper metabolic scaling than do related benthic species (or life-stages), possibly because of age- and size-specific differences in locomotor costs, cellular mode of growth, or predation-caused rates of mortality, growth and reproduction. Opposite patterns are shown for teleost fishes, possibly owing, at least in part, to their lesser vulnerability to predation (associated with their larger body size and more rapid escape movements), and to their using swim-bladder supported buoyancy to avoid added energy costs of locomotion in open water	[20,24,28,35,36,39]
food habits	complex	termites, birds and mammals with different food habits exhibit different metabolic scaling relationships. Invertebrate-eating mammals show shallower metabolic scaling than vertebrate-eating mammals, perhaps because large mammals cannot sustain a high metabolism on a diet of small invertebrates	[2,4,34,139–141]

(*Continued.*)

Table 1. (*Continued.*)

interactive effects of intrinsic and extrinsic factors			
type	**direction of interactive effect**[a]	**underlying mechanism**	**selected sources**
habitat/microhabitat	complex	interspecific metabolic scaling varies with type of habitat or microhabitat. Steeper mass-scaling of metabolic rate in birds and mammals from xeric versus mesic habitats, subtidal versus intertidal marine snails, and burrowing versus non-burrowing terrestrial earthworms and marine crustaceans may be explained by the MLBH, where a higher mass-scaling exponent is associated with a lower metabolic level [23,24]	[4,20,24,114,142–146]
body size and captivity	negative	in birds, small species upregulate their metabolism in captivity, whereas large species downregulate their metabolism, possibly in association with the food quantity and/or quality offered in captivity	[147]
body size and geographical location (latitude and altitude)	variable	mass-scaling of whole-body metabolism depends on geographical location. Scaling exponents tend to be higher in cooler environments, which may be partly owing to shifts in the relative influence of volume- versus surface area-related metabolic processes, as predicted by the MLBH [23,24]. However, exponents below two-thirds in warm environments require further explanation	[144,148–155]
body size and season	variable	metabolic scaling may vary with season, possibly because of changes in size-specific production costs (owing to changing rates of growth and reproduction) or activity levels	[156–167]
body size and abiotic environmental factors			
temperature	negative for resting, but could be positive for active metabolic rate	mass-scaling exponents for metabolism tend to decrease with increasing temperature, which may be owing to shifts in the relative influence of volume- versus surface area-related metabolic processes, as predicted by the MLBH [23,24]. Other patterns may be the result of interactive influences of activity level or growth rate [23,61]	[20,24,28,33,120,128,133, 158,167–191]
pH (CO_2)	positive (negative)	mass-scaling exponents for metabolism in aquatic animals tend to decrease with decreasing pH (or increasing CO_2), which may be owing to the metabolism of large individuals being more sensitive to increased acidity than that of small individuals	[185,192]
salinity	variable (size-specific)	effects of decreased salinity on metabolic rate varies with body size, possibly, at least in some cases, owing to size-specific costs of ionic regulation that vary with body surface area to volume ratios	[193–195]
oxygen supply	variable (size-specific)	the mass-scaling exponents for metabolic rate may show a positive, negative or humped relationship with increasing oxygen supply. The metabolism of relatively large animals with relatively low surface area to volume ratios may be more affected by hypoxia than that of smaller organisms. Size-specific variation in aerobic and anaerobic metabolism may also be important	[24,84,196–199]
water supply	complex	the mass-scaling exponents for photosynthetic rate in two plant species varied with water supply	[200]
light intensity	negative	in aquatic animals, light increases the metabolic rate of small individuals more than that of large individuals	[201,202]

(*Continued.*)

Table 1. (*Continued.*)

interactive effects of intrinsic and extrinsic factors			
type	**direction of interactive effect**[a]	**underlying mechanism**	**selected sources**
day/night	negative	in sandy beach amphipods and isopods, the mass-scaling exponent for metabolic rate is greater during night (active time) than day (resting time)	[57,58,203]
pollution	negative	pollution causes a greater decrease in metabolic rate in small versus large bivalves	[165]
exposure to air versus water	variable (size-specific)	in aquatic/intertidal animals, the mass-scaling exponents for metabolic rate may increase or decrease from water to air, possibly as a function of relative adaptation to terrestrial versus aquatic life, and thus the relative effectiveness of respiration in air versus water	[204–209]
body size and biotic environmental factors			
predation	variable (size-specific)	in an aquatic amphipod, the presence of fish predators caused the metabolic rate of relatively large adults to decrease, but to increase or stay the same in smaller juveniles	[70,76]
parasites	negative	parasitic infections reduce the metabolic rate of large snails more than that of small snails	[210]
food quantity/quality	variable (size-specific)	effects of food quantity or quality on metabolic rate depend on body size	[72,128,166,211–219]
life-history stage and extrinsic factors			
temperature	complex	effects of temperature on metabolic rate depend on life-history stage	[220]
oxygen	variable (age-specific)	sensitivity of metabolic rate to hypoxia varies with developmental (life-history) stage	[84]
light intensity	variable (age-specific)	sensitivity of metabolic rate to light varies with developmental (life-history) stage	[202]
growth rate and extrinsic factors ration level	positive	metabolic rate and growth rate are positively correlated at relatively high, but not low ration levels	[221–223]
behaviour and extrinsic factors	variable	relationships between metabolic rate and behavioural traits vary with temperature, hypoxia, food supply, conspecific density, cover, water velocity, and season	[224,225]
colony composition and extrinsic factors			
ration level		metabolic rate of honeybees is interactively affected by colony composition and resource level	[226]
temperature and intrinsic factors			
genotype	variable (genotype-specific)	temperature sensitivity of metabolic rate varies with genotype. In a butterfly, the metabolism-temperature relationship is positive for homozygotes and negative for heterozygotes	[227]
cell size	variable (cell-size-specific)	increasing temperature increases metabolic rate more in fishes with small versus large cells, probably because of surface area to volume constraints at the cellular level	[228]
activity level	variable	effects of temperature on metabolic rate vary with activity level and vice versa	[24,169,229–231]

(*Continued.*)

Table 1. (*Continued.*)

interactive effects of intrinsic and extrinsic factors			
type	**direction of interactive effect**[a]	**underlying mechanism**	**selected sources**
body size and multiple interacting extrinsic factors			
temperature and predation	variable (size-specific)	fish predation cues/regime affect how temperature influences the mass-scaling of metabolic rate in aquatic amphipods. This interactive effect may be the result of differences in size (age)-specific mortality (and associated size-scaling of metabolically expensive growth and behavioural activity) between habitats with and without visually hunting fish predators	[232,233]
temperature and pH	variable (species-specific)	temperature effects on the mass-scaling of metabolic rate in aquatic animals depend on pH, possibly owing to size-specific energy costs of stress responses to acidity	[185,234]
temperature and oxygen	complex	developing zebrafish show complex interactions between acute and chronic effects of temperature and hypoxia on metabolic rate and its scaling with body mass. Larger protists show a greater increase in metabolic rate with increased oxygen supply, but lesser increase in metabolic rate with increasing temperature than do smaller protists	[127,235]
temperature and salinity	variable (species-specific)	temperature effects on mass-scaling of metabolic rate in aquatic animals depend on salinity, possibly owing to size-specific energy costs of ionic (osmotic) regulation	[195]
temperature and nutrition	negative	temperature effects on mass-scaling of metabolic rate may depend on nutrition. In a marine isopod, starvation suppressed the metabolism of small individuals more than that of large individuals, especially at high temperatures	[212]
temperature and exposure to air versus water	variable	in intertidal animals, temperature effects on mass-scaling of metabolic rate may depend on whether respiration is in air or water	[204]
temperature and phylogenetic affinity	variable	thermal responses of metabolic rate may vary among species and higher taxa	[236,237]
temperature and multiple interacting intrinsic factors			
body size and activity level	variable	temperature effects on the mass-scaling of metabolic rate may vary with activity level. Increased temperature tends to cause the mass-scaling exponent for resting metabolic rate to decrease, but if increased temperature causes increases in behavioural activity, the metabolic scaling exponent may increase, as predicted by the MLBH [23,24]. Also, at low temperatures, increased activity may cause less change in the metabolic scaling exponent than that seen at high temperatures	[24,169]
body size and thermoregulatory mode	negative (ectotherms) positive (endotherms)	temperature effects on the mass-scaling exponent for metabolic rate depend on thermoregulatory strategy (ectothermy versus endothermy)	[33]
body size and genotype	complex	temperature effects on the mass-scaling of metabolic rate depend on genotype (banded versus unbanded morphs) of a terrestrial snail	[44]

(*Continued.*)

Table 1. (*Continued.*)

interactive effects of intrinsic and extrinsic factors			
type	**direction of interactive effect[a]**	**underlying mechanism**	**selected sources**
salinity and multiple interacting intrinsic factors			
body size and activity level	variable	salinity affects how the mass-scaling of metabolic rate changes with activity level	[193,194]

[a]Positive effects are synergistic, whereas negative effects are antagonistic.

intensity of R or its 'metabolic level' (L), which is a measure of the elevation of a metabolic scaling relationship [23]. L depends on the intensity of various resource-demanding processes, such as growth, reproduction, thermoregulation, locomotion and food processing. In isomorphic organisms with similar body shapes and compositions, the scaling exponent b is predicted to vary between two-thirds and 1, depending on L. For resting metabolic rates (RMRs), when L_{RMR} is high (as in high-energy endothermic birds and mammals), SA-related metabolic processes related to resource supply and/or metabolic waste removal (including heat dissipation) should predominate, thus causing b to approach two-thirds, as often observed [21,23,24,28,29,168]. However, when L_{RMR} is low and not limited by SA-related resource supply or metabolic waste removal (as in low-energy ectothermic organisms and during diapause, torpor, or hibernation), V-related metabolic processes involving tissue maintenance should predominate, thus causing b to approach 1, as often observed [21,23,24,28,29,168]. Furthermore, for active metabolic rates (AMRs), when L_{AMR} is high as a result of heightened V-related resource-demanding processes, such as growth, locomotion and food-processing (specific dynamic action) that appear to involve metabolic processes pervading many or all of the tissues of the body, b should approach 1, as again often observed [21–24,30]. Overall, for both RMRs and AMRs, the MLBH predicts a concave upward relationship between b and L, as observed in chitons, insects, fishes, birds and mammals [21,23,24,31]. Therefore, the MLBH can help explain several of the interactive effects on metabolic rate that involve body size, including the modulating effects of activity level, mode of locomotion, mode of thermoregulation, growth rate, food processing and reproductive state (table 1).

The CMT, which embraces the MLBH, includes four major modal mechanisms: SA-related fluxes of resources and wastes (including heat), physical constraints of internal resource transport on resource supply, body composition and various processes affecting resource demand [8,27]. The effects of cell size and cellular mode of growth on the body-mass scaling exponent b can be explained in terms of geometric constraints of cellular SA/V ratios on resource uptake and transport. According to the cell-size theory of metabolic scaling, if growth in size during ontogeny or evolution is mainly owing to increases in cell size, b should be near two-thirds, whereas if growth in size is mainly owing to increases in cell number (thus maintaining a constant ratio of cellular SA to body V), b should be near 1. If growth in size is owing to increases in both cell size and number, then b should be between two-thirds and 1. Evidence for these predicted patterns has been provided by [32,37–40]. Furthermore, the effects of genome size (which is highly correlated with cell size: reviewed in [240]) on b can also be explained by cell-size theory [32,39,41].

Geometric constraints related to SA/V ratios can also explain how body shape interacts with body size to influence metabolic rate. Growth primarily in one or two of the longest dimensions (elongation and flattening, respectively) allows SA/V ratios to remain constant (rather than declining as $M^{-1/3}$, as observed with isomorphic growth), thus permitting the mass-scaling exponent for metabolic rate to approach 1, as observed in several pelagic skin-breathing invertebrates [69,80,105]. By contrast, growth primarily in the shortest dimension (thickening), as occurs during the early development of very slender American eels (*Anguilla rostrata*), is related to b values lower than two-thirds [81].

In addition, changes in body composition (among other factors) can help explain why the mass-scaling exponent (b) for metabolic rate may change with developmental (life-history) stage. Shifts in the relative masses of tissues with high versus low metabolic rates can significantly alter how metabolic rate relates to body size [8,82,83]. Differences in size-specific body composition may also help explain some cases where the metabolic scaling exponent b differs between the sexes (as in humans [48]).

3. Interactive effects of extrinsic factors

Temperature is the most important extrinsic factor affecting metabolic rate. Indeed, the effect of temperature on the rate of metabolism and other biological processes has often been well described by the exponential van't Hoff-Arrhenius function $e^{-E/kT}$ (where E is the apparent activation energy, k is Boltzmann's constant and T is temperature in Kelvin), or by equivalent Arrhenius plots [17,18,241–243] or other mathematical coefficients [15,244]. However, as also seen for the body-mass scaling of metabolic rate (see §2), the temperature scaling of metabolic rate is highly malleable, as revealed by significant effects of salinity, pH (CO_2), oxygen supply, food supply, toxicants, microplastics, latitude, altitude and ecological lifestyle on the temperature sensitivity of metabolic rate (table 1).

Many of these interactive effects involve increased resource availability (thus facilitating temperature-related increases in metabolic rate), heightened metabolic costs of specific biological processes, or metabolic acclimation/adaptation in environments with different temperature regimes (also table 1). For example, increased oxygen supply, especially in water, may allow metabolic rate to increase more easily with increased temperature, without harmful effects of hypoxia (though interactive effects of temperature and oxygen on metabolic rate can be complex [235] and deserve further investigation [245]). Increased food supply may similarly permit greater scope of change in metabolic rate in response to increased temperature. In addition, stressful impacts of extreme salinity or pH, or the presence of harmful toxicants and microplastics may heighten metabolic costs related to specific biological processes, such as ionoregulation, osmoregulation or tissue repair, thus altering temperature responses of metabolic rate. Furthermore, enhanced temperature responses of metabolic rate exhibited by conspecific organisms from higher latitudes or altitudes may be the result of metabolic acclimation/adaptation to cooler environments (see [132,136] and other references in table 1).

Light and predator cues also have interactive effects on metabolic rate. In light, fish predator cues significantly alter the metabolic rates of aquatic amphipod crustaceans, but not in the dark [138]. This interaction makes adaptive sense, because amphipods are more vulnerable to predation by visually hunting fishes when it is light, than when it is dark.

4. Interactive effects of intrinsic and extrinsic factors

Given the importance of body mass and temperature T in influencing metabolic rate (as discussed in §§2 and 3), it is not surprising that interactions between these two 'hub factors' are among the most common examples of interactive effects of intrinsic and extrinsic factors on metabolic rate. Numerous studies have shown that the mass-scaling exponent b of metabolic rate varies significantly with T (reviewed in [20,24,27,169]). In plants and resting ectothermic animals, b often decreases with increasing T, presumably because of the increasing influence of SA-related metabolic processes at high L, as predicted by the MLBH ([24,28,133,169,170] and other references cited in table 1). By contrast, in actively growing or moving ectothermic animals, b may increase with increasing T, or show other patterns of covariation with T [24,169]. In addition, although cold exposure often causes b to increase in ectothermic animals (approaching 1, owing to the increasing influence of tissue V-related metabolic processes), the opposite occurs in endothermic birds and mammals, where b approaches 0.5, which approximates the scaling exponent for thermal conductance [33]. Other extrinsic effects on b, such as those owing to geographical location, may also be explained by temperature effects on b. According to the MLBH, metabolic scaling relationships exhibited by populations of ectotherms at cooler latitudes and altitudes should have lower L values, and thus higher b values, as often observed (see table 1).

Temperature effects on metabolic rate may also be altered by various intrinsic factors, such as genotype, cell size and activity level, independently of body size. For example, increasing temperature increases metabolic rate more in fishes with small versus large cells, probably because of SA/V constraints at the cellular level [228].

Other examples of interactive effects of intrinsic and extrinsic factors on metabolic rate include significant effects of pelagic versus benthic life styles, food habits, habitat/microhabitat, captivity, season, pH (CO_2), salinity, oxygen supply, water supply, light intensity, day versus night, pollution, exposure to air versus water, predation, parasites and food quantity/quality on the mass-scaling exponent (b) for metabolic rate (table 1). Mechanisms involved in these interactive effects may include size-related geometric (SA/V) constraints on resource uptake and waste removal, or size-related variation in the effects of different food quantity/quality or of various resource-demanding biological processes. For example, according to the MLBH, some habitat/microhabitat effects on b may be explained by differences in the relative influence of SA- versus V-related metabolic processes, which are a function of metabolic level (L). In particular, when L increases (and SA-related metabolic processes are expected to become more important), as observed with transitions from xeric to mesic habitats, subtidal to intertidal microhabitats, and burrowing to non-burrowing habits, b decreases, as predicted (also see [8]). Other extrinsic effects on b, such as effects of season, day versus night, and pelagic versus benthic life styles have been attributed to size-related differences in the metabolic costs of various resource-demanding processes, such as growth, reproduction and behavioural activity.

Life-history stage may also interact with various extrinsic factors, such as temperature, oxygen and light intensity, to affect metabolic rate. Apparently, the metabolic rates of different life-history stages show different sensitivities to warming, hypoxia and increased light intensity (table 1). For example, in intertidal porcelain crabs (*Petrolisthes laevigatus*), the metabolic rate of adults varies less in response to hypoxia than does that of earlier life-history stages. These differences have been attributed to greater homeostatic regulatory ability in more mature crabs [84].

Three-factor interactive effects have also been documented. For example, extrinsic factors such as predation, pH (CO_2), salinity, nutrition and exposure to air versus water can modify the effect of temperature on the mass-scaling exponent (*b*) for metabolic rate (table 1). In particular, fish predator cues or habitat regime significantly alter the effect of temperature on the mass-scaling exponent (*b*) of freshwater amphipods, apparently because of ontogenetic shifts in metabolically expensive processes such as growth and behavioural activity, ultimately caused by differences in size (age)-specific mortality between habitats with and without fish predators [232,233]. Salinity also affects how the mass-scaling of metabolic rate varies with activity level in freshwater fishes [193,194].

5. Overview of interactive effects and their mechanistic causes

Most of the interactive effects documented in our review involve two factors. Relatively few involve three factors; and we are not aware of any examples involving four-factor interactive effects. The challenges of testing for three- or four-factor interactive effects are daunting. However, such studies may allow us to gain a better understanding of how various factors realistically affect the metabolic rate of organisms in nature, where complex networks of ecological interactions occur. For example, the effect of temperature on the mass-dependence of metabolic rate in aquatic amphipods is completely the opposite depending on whether fish predators or their chemical cues are present or absent [232,233].

Although we have identified body size and temperature as 'hub factors', further research may reveal that other intrinsic and extrinsic factors, such as cell size, activity level, life-history stage and resource (food and oxygen) availability, have sufficiently general influences on metabolic rate to be called hub factors, as well. Cell size (and its correlate genome size) may importantly influence metabolic rate in multiple ways, including via geometric (SA/V) constraints on cellular resource supply and effects of cell-size-related cellular processes and composition on resource demand [39,246]. Activity level has profound influences on resource demand that influence variation in metabolic rate, both with and independently of body size [19–24,169]. The influence of many intrinsic and extrinsic factors can vary significantly with life-history (developmental) stage. Ontogenetic changes in various intrinsic factors, such as body shape/composition, the cellular mode of growth, anaerobic versus aerobic mode of metabolism, and rates of energy-demanding growth, reproduction, thermoregulation and behavioural activity can profoundly affect organismal metabolic rate and its scaling with body size (table 1). In addition, the metabolic rate of early ontogenetic stages may be affected more/less by extrinsic factors, such as temperature, oxygen availability and light intensity, than are later ontogenetic stages (see table 1). Therefore, it is important that experimental and comparative studies of biological and environmental effects on metabolic rate consider not just adults, but also immature life stages [10]. Since metabolic rate is fuelled by environmental resources, resource quantity/quality is also a critical factor that should be given increased attention (e.g. [34,247–252]). Laboratory studies of individual and species variation in metabolic rate that are based on ad libitum food conditions may not well represent the natural conditions that organisms routinely face.

Finally, although hypothetical mechanisms for several interactive effects have been identified (table 1), we still know little about the mechanisms underlying many other interactive effects (e.g. interactive effects of body size with genotype, gender and reproductive strategy, of temperature with genotype, acidity and toxicants, and of life-history stage with temperature, oxygen supply and light intensity). Moreover, the hypothetical mechanisms that have been identified are based mostly on proximate functional causes, which may vary between major habitats and life-styles (e.g. aquatic versus terrestrial species [22,169]). We still have much to learn about the ultimate evolutionary causes for some interactive effects, especially those involving interactive effects of body size with phylogenetic affinity, ecological life style, life-history stage, reproductive strategy and exposure to predators, of temperature with latitude, altitude, ecological life style and phylogenetic affinity, and of life-history stage with various extrinsic factors. Exploring the relative roles of biological regulation, adaptive evolution and genetic/developmental/physical constraints in causing interactive effects on metabolic rate represents a new, exciting frontier of research.

6. Theoretical and practical implications

Recognition of interactive effects on metabolic rate has important theoretical and practical implications. For example, theoretical models based on the 3/4-power law of metabolic scaling, or the independent effects of only one or two major factors (e.g. body size and temperature, as in the MTE) require modification, so that they may more realistically predict and explain variation of the rate of metabolism and other metabolically dependent biological processes in nature. Our review reaffirms the importance of variation in body size and temperature in causing variation in metabolic rate, but also shows that many other intrinsic and extrinsic factors interact with these factors and each other in substantial ways to affect metabolic rate (figures 1 and 2, table 1). To explain these effects, multi-mechanistic models that embrace various contingent effects should receive increased attention, as has been promoted by several investigators with respect to the diversity of metabolic rate and its scaling with body size (e.g. [1,8,9,27,34,253–256]).

Our review highlights the complex, intimate interrelationships between physiology and ecology, knowledge of which should increase our understanding of various phenomena in both disciplines. Knowing how various intrinsic and extrinsic factors interactively affect the metabolic rate of organisms may enhance our understanding of not only why organisms exhibit diverse physiological adaptations in different environments but also how their metabolic physiology may have shaped their life histories, ecological niches, and interactions with various abiotic and biotic environmental factors in ecosystems (also see [257–259]). For example, limited genetic variation, evolvability and/or phenotypic plasticity of metabolic rate may potentially limit the niche space and geographical range of a species (e.g. [260–262]).

Important practical applications of a knowledge of pervasive interactive effects on metabolic rate include (i) devising better ways to 'correct' for effects of body size and temperature on rates of metabolism and other biological processes in comparative analyses, (ii) making more realistic predictions of effects of climate change on organisms and

ecological systems, (iii) improving our understanding of how various factors affect size-abundance relationships in populations and communities, and (iv) refining estimations of drug dosages in humans and animals of different age. Possible methods for including interactive effects between body size and various intrinsic and extrinsic factors in comparative analyses that attempt to correct for the effects of body size on metabolic rate and other traits, have been reviewed by [25]. Studies that attempt to correct for effects of temperature on metabolic rate should also consider interactive effects. Including interactive effects of various intrinsic and extrinsic factors would also improve efforts to link physiological measurements with organismal performance in natural environments. In particular, predictions of how organisms, populations and communities respond to climate change would be made more realistic and reliable by including interactive effects. This view is supported by the many studies showing interactive effects between temperature and several other factors on metabolic rate (table 1). In addition, predictions of size–abundance relationships in populations and communities could be made more accurate by considering interactive multi-factor effects on size-metabolism relationships that are thought to underlie size-abundance relationships, at least in part. Lastly, the accuracy of dosage levels for drugs administered to humans and animals could be improved by considering interactive effects between body size and life-history stage on metabolic rate. Mass-scaling relationships for metabolic rate (and similarly rates of drug clearance) differ significantly between children (juveniles) and adults [8,82,85,263,264].

7. Conclusion and prospects

We conclude that a holistic system view of metabolic rate, involving interactive multi-directional causal networks, is much needed. Metabolic rate is a 'hub trait' (or 'super-trait' [259]) with body size and temperature being major influential 'hub factors' that are, in turn, affected by many other intrinsic and extrinsic factors, such as cell size, activity level, life-history stage, the supply and demand for various kinds of resources (including food and oxygen), ecological life style, habitat and various biotic and abiotic environmental factors (figures 1 and 2). Holistic system analyses of metabolic rate should include interactive proximate and ultimate mechanisms operating at multiple hierarchical levels of biological organization. As a result, our understanding of how and why metabolic rate varies so much among organisms in nature should be much improved.

Data accessibility. This article has no additional data.

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.S.G.: conceptualization, resources, visualization, writing—review and editing; V.G.: conceptualization, resources, visualization, writing—original draft, writing—review and editing.

Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

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