Ecology shapes metabolic and life history scalings in termites

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Abstract. 1. Metabolic rate (B) is a fundamental property of organisms, and scales with body mass (M) as $B = \alpha M^{\beta}$. There has been much debate on whether scaling parameters should be viewed as constants or variables. However, there is increasing evidence that ecological differentiation can affect both α and β.

2. In colonial organisms such as social insects, individual metabolism is integrated at the colony level. Theory and data suggest that whole-colony metabolism partly reflects individual-level metabolic and life-history scalings, but whether these have been affected by ecological diversification is little known.

3. Here, this issue was addressed using termites. Data from the literature were assembled to assess the interspecific scalings of individual metabolic rate with individual mass, and of individual mass with colony mass. Concurrently, it was tested whether such scalings were affected by two key ecological traits: lifestyle and diet.

4. Individual-level metabolic scaling was affected by diet, with $\beta = 1.02$ in wood feeders and 0.60 in soil feeders. However, there was no difference in α. Further, individual mass scaled to the 0.25 power with colony mass, but forager species had larger colonies and smaller individuals relative to wood-dwelling, sedentary ones, thus producing a grade shift.

5. Our results show that ecological diversification has affected fundamental metabolic and life-history scalings in termites. Thus, theory on the energetics and evolution of colonial life should account for this variability.

Key words. Allometry, comparative analysis, ecological niche, eusociality, Isoptera, metabolic-level boundaries hypothesis.

Introduction

Life depends on converting resources to power to sustain its structure and function, i.e. metabolism. As resources are limited, metabolic rate (B) should have important ecological and evolutionary implications (Milewski & Mills, 2010). B has long been shown to scale with body mass (M), as described by the allometric equation $B = \alpha M^{\beta}$ (Kleiber, 1932). Kleiber suggested that β approximated 0.75 in both intra- and interspecific comparisons, which eventually gained the status of 'law' (Hulbert,

2014). However, many studies have documented consistent variation in both α and β among taxa, suggesting that Kleiber's 'law' is a statistical average rather than a universal constant (White *et al.*, 2007; Makarieva *et al.*, 2008; Isaac & Carbone, 2010; Ehnes *et al.*, 2011; Hulbert, 2014).

While a number of hypotheses have been advanced to account for variability in interspecific metabolic scaling (reviewed by White & Kearney, 2013; Glazier, 2014), there is increasing evidence that species ecological traits can shape their metabolic rates. This idea has been made explicit by the metabolic-level boundaries hypothesis (MLBH) (Glazier, 2005, 2010, 2014), which posits that ecological variation between organisms affects their 'metabolic level' (i.e. elevation of metabolic scaling, α), which in turn affects β. Two ecological traits have been generally

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studied in this regard: lifestyle and diet (McNab, 2007; White & Kearney, 2013; Glazier, 2014). First, species with more active lifestyles tend to have higher metabolic rates (Huey & Pianka, 1981; Reinhold, 1999; Muñoz-Garcia & Willias, 2005; Killen *et al.*, 2010; Glazier, 2014). Second, there is some evidence that species feeding on more recalcitrant substrates (e.g. plant relative to animal tissue) tend to have higher metabolic rates (Marsden *et al.*, 2012; Naya *et al.*, 2013), although the opposite has also been reported, and diet and activity level can be correlated (Huey & Pianka, 1981; Munõz-Garcia & Williams, 2005). In both cases, however, metabolic rate has been suggested to relate to species ecology through changes in body tissue composition. Most metabolic costs are attributable to the maintenance of visceral and muscular tissue (White & Kearney, 2013), the relative size of which has been shown to predict resting metabolic rates across species (Raichlen *et al.*, 2010; Williams *et al.*, 2010). Accordingly, it has been suggested that higher metabolic rate in more active species would reflect greater investment in muscular tissue (Reinhold, 1999; Muñoz-Garcia & Willias, 2005; Killen *et al.*, 2010; Glazier, 2014), whereas higher metabolic rate in herbivore species would reflect greater investment in gut tissue (Karasov *et al.*, 2011; Naya *et al.*, 2013).

Given this variation, the MLBH posits that the metabolic rate of an organism with high α is primarily constrained by the surface area available for exchanging nutrients, wastes and heat. As body surface scales as $M^{2/3}$ in geometrically similar organisms, β should tend towards 2/3 or 0.67. Conversely, when α is low, the MLBH suggests that surface-related fluxes are no longer limiting, and metabolism reflects mainly the total maintenance cost of volume-filling tissues. As this cost is directly proportional to body volume or mass, β should tend towards 1. Thus, β should decrease from 1 to 0.67 as α increases, a prediction that has been generally supported (Glazier, 2005, 2010, 2014; Killen *et al.*, 2010).

Metabolic scaling has been primarily addressed in unitary organisms. Yet, many organisms live in colonies with high functional integration among individuals. Indeed, colonial organisms such as ants and termites dominate many terrestrial ecosystems in terms of biomass and ecological impact (Bourke, 1999; Hölldobler & Wilson, 2009; Dornhaus *et al.*, 2012). Colony metabolism comprises the metabolism of many individuals, but little is known about how individual metabolism itself is reflected in colony function. While some have suggested that whole-colony metabolic scaling complies to a single, universal exponent (Hou *et al.*, 2010), there is increasing evidence of variability in colony-level β (Waters, 2014), possibly due to ecological factors (Shik *et al.*, 2014). Still, reports on whole-colony metabolic scaling often indicate negative allometry ($\beta < 1$). This has been attributed, at least in part, to an observed positive scaling of individual mass with colony mass; this, coupled to the negative allometry typical of individual-level metabolic scaling, is sufficient to cause larger colonies to have relatively lower metabolic rates (Shik, 2010; Shik *et al.*, 2012; Waters, 2014). In contrast, sociobiological models typically assume a trade-off in social resource allocation, where societies invest in either many small individuals or fewer, larger ones (Jaffe & Deneubourg, 1992; Karsai & Wenzel, 1998; Bourke, 1999; Nalepa, 2011; van Oudenhove *et al.*, 2013; Feinerman & Traniello, 2015).

Thus, there is considerable uncertainty on the scalings among metabolic rate, individual mass and colony mass, as well as on the extent to which they are shaped by ecological differentiation.

Most research on allometric scaling of colonial organisms has focused on ants. Termites are the oldest known eusocial animals, and despite having followed a path to eusociality different from that of ants, they have achieved comparable ecological success (Howard & Thorne, 2011). Negative allometry has also been found in termite colony-level metabolic scaling, although comprehensive data are only available for a single species (Jaffe, 2010). However, while at coarse taxonomic levels there is a general increase in colony size from the termite ancestor to more derived clades (Lepage & Darlington, 2000), body size seemingly followed the opposite trend (Nalepa, 2011). This contrasts with the positive scaling between these traits reported for ants (King, 2010; Shik *et al.*, 2012; Mason *et al.*, 2015). Furthermore, estimates of individual-level metabolic scaling across termite species are highly conflicting (Wood & Sands, 1978; Wheeler *et al.*, 1996; Bignell *et al.*, 1997; Jeeva *et al.*, 1999) and a recent analysis even suggested that termite metabolic scaling differs fundamentally from that of other insects (Riveros & Enquist, 2011). Such uncertainties may be due to the marked diversification in lifestyle and diet that termites have experienced (Eggleton & Tayasu, 2001; Korb, 2007; Bourguignon *et al.*, 2011), as suggested by the MLBH. Addressing this issue should advance metabolic theory, especially in the context of colonial life.

Here, we used the MLBH as a framework to investigate the effects of lifestyle and diet on the interspecific scalings of: (i) individual metabolic rate with individual mass and (ii) individual mass with colony mass in termites. We synthesised the available, relevant literature data and tested the following specific hypotheses:

1   *Lifestyle affects metabolic scaling*. Most basal termite families have a sedentary lifestyle (also known as 'lifetype' in the termite literature), in which species both nest and feed on a single wood piece and helper activities are performed by undifferentiated nymphs, the pseudergates (Roisin, 2006; Korb, 2007; Roisin & Korb, 2011). Conversely, more derived clades feature mainly a forager lifestyle, in which colonies build a defined nest from which a specialised worker caste forages (Roisin, 2006; Korb, 2007; Roisin & Korb, 2011). Thus, we expected forager species to have a high α relative to sedentary species, given their more active lifestyle. Accordingly, β should be lower in forager species relative to sedentary ones. We tested estimated slopes against the boundary values of 0.67 and 1 predicted by the MLBH as reference points.

2   *Diet affects metabolic scaling*. While basal termite families feed strictly on wood, the largest, more derived family (Termitidae) comprises species feeding along a humification gradient, from wood to mineral soil (Eggleton & Tayasu, 2001; Bourguignon *et al.*, 2011). On the one hand, this trophic divergence correlates with digestive morphology: soil feeders have longer guts with more compartments relative to wood feeders (Bignell & Eggleton, 1995), in which case we would expect soil feeders to have a higher α

and a lower β than wood feeders due to larger investment in visceral tissue (Karasov *et al.*, 2011; Naya *et al.*, 2013). On the other hand, wood feeders forage for a patchily distributed resource, and generally move faster and for longer distances relative to soil feeders, the resource of which is ubiquitous (Eggleton *et al.*, 1998). Thus, it is equally plausible to expect wood feeders to have a higher α and a lower β than soil feeders, due to larger investment in muscular tissue (Muñoz-Garcia & Willias, 2005; Killen *et al.*, 2010). Again, we tested estimated slopes against the reference slopes of boundaries of 0.67 and 1 predicted by the MLBH.

3 *Lifestyle affects the scaling of individual mass with colony mass*. Theory and data suggest that negative allometry in colony-level metabolic scaling results partly from a joint increase in individual and colony mass (Shik, 2010; Shik *et al.*, 2012; Waters, 2014; Mason *et al.*, 2015). Thus, we predicted a positive scaling of individual mass with colony mass in termites. However, we expected this relationship to be affected by lifestyle. On the one hand, sedentary termites eventually deplete their food; thus, selection favours developmental flexibility (as pseudergates) to allow dispersal (as alates) under resource shortage (Roisin, 2006; Rupf & Roisin, 2008; Roisin & Korb, 2011). On the other hand, forager termites minimise starvation risk by foraging away from the nest; thus, selection favours foraging efficiency, i.e. a large, specialised workforce (Roisin, 2006; Rupf & Roisin, 2008; Roisin & Korb, 2011). Therefore, the scaling of individual mass with colony mass should shift towards larger colony mass from sedentary to forager termites.

Materials and methods

Data assembly

We gathered data from previous compilations, which were complemented with individual studies (File S1; Tables S1 and S2). The final dataset covered most families and subfamilies currently recognised (Krishna *et al.*, 2013). Measurements of individual-level metabolic rate and the respective body mass were extracted from published tables for 50 species, and predicted from body mass for another 13 species using a published regression equation with high predictive power ($r^2 = 89\%$) (Wheeler *et al.*, 1996). Sensitivity analysis showed that our results were robust to the known uncertainty in such predictions (File S1, Figure S1). All measurements were taken from workers or pseudergates (depending on species), which comprise the bulk of colonies. For species showing worker dimorphism ($n = 3$), we considered the most abundant form. We assumed such data to represent resting conditions, as indicated by an observed decrease in respiration rate following termite incubation (Bignell *et al.*, 1997). Measurements were either in $\mu mol\,O_2\,g^{-1}\,h^{-1}$ or in $\mu l\,O_2\,h^{-1}$. To standardise units, we converted mass-specific measurements to whole-body values by multiplying by body mass, and then to $\mu l\,O_2\,h^{-1}$ by assuming $1\,mol = 22.4$ litres. Lastly, we adjusted all measurements to a standard temperature ($25\,^\circ C$) if taken at a different one (T) by multiplying by $Q_{10}^{(25-T)/10}$, with $Q_{10} = 2$ (Makarieva *et al.*, 2008).

The average individual mass of species was primarily estimated as the average wet mass of workers (mg), as it has been most frequently reported ($n = 19$). When a range was provided, we used the mean. For species showing worker dimorphism, we considered the most abundant form ($n = 6$). When a true worker caste did not occur in the species, we used the average mass of pseudergates, which predominate in colonies of workerless species ($n = 13$). If worker/pseudergate data were not available, we used the ratio between the densities of biomass and individuals when reported by the same study as an estimate of average individual mass ($n = 10$). If such an estimate was available from more than one source for the same species, we calculated their average weighted by their respective individual densities. In the few cases in which only worker dry mass was reported ($n = 4$), the average mass of individual workers was estimated from a regression between worker wet (Y) and dry mass (X) for those species in which both measures were available ($\log_{10}Y = 0.51 + 1.04\,\log_{10}X$, $r^2 = 87\%$, $n = 16$).

Given the paucity of published measurements of termite colony mass, we compiled data on average number of individuals per colony (except eggs), and then estimated average colony mass (g) by multiplying the former by average individual mass. We defined quality criteria for including data, due to the variety of methods employed in the literature. First, we preferred direct counts of field colonies, either complete counts or extrapolations from colony subsamples. We did not consider estimates from mark–recapture methods, as these have been shown to be highly unreliable when applied to termites (Evans *et al.*, 1998, 1999). Second, we only considered estimates of colony size with known sample sizes and for which the number of sampled colonies was equal to or higher than five (in a single study or across studies on the same species). If different studies reported data on the same species, we used their average weighted by the number of colonies sampled in each study. For two species, only estimates of maximum colony size were available, but we found that average (Y) and maximum colony sizes (X) were strongly correlated ($\log_{10}Y = -0.54 + 1.03\,\log_{10}X$, $r^2 = 96\%$, $n = 39$). Thus, we predicted the average colony size of these species from their maximum.

Species were classified in one of two lifestyles based on literature data: 'sedentary', if both nesting and feeding on the same resource patch; or 'forager', if gathering food outside the nest site and returning it to the nest (Roisin, 2006; Korb, 2007; Roisin & Korb, 2011). Although more detailed classification schemes have been proposed (Eggleton & Tayasu, 2001), adopting any of them would render our sample highly unbalanced between categories. Yet, the sedentary/forager dichotomy correlates well with key evolutionary transitions in termite life history and social organisation and is thus biologically informative (Roisin, 2006; Korb, 2007; Roisin & Korb, 2011). Further, we classified each species as wood or soil feeder, as reported in the literature. Ideally, one would use a quantitative measure of trophic level, such as stable isotope signatures (Bourguignon *et al.*, 2011), but these are available for few species. Nonetheless, stable isotope analysis supports a broad differentiation between predominantly wood- and soil-feeding species, as opposed to alternative classification schemes of trophic niche (Bourguignon *et al.*, 2011).

Table 1. Reference model set used to analyse the scalings of individual metabolic rate with individual mass, and individual mass with colony mass in termites.

Model description	Model notation
No scaling	a
Single α and β	$a + b_1 M$
Lifestyle affects α	$a + b_1 M + b_2 L$
Diet affects α	$a + b_1 M + b_3 D$
Lifestyle and diet affect α	$a + b_1 M + b_2 L + b_3 D$
Lifestyle affects β	$a + b_1 M + b_2 L + b_4 (M \times L)$
Diet affects β	$a + b_1 M + b_3 D + b_5 (M \times D)$
Lifestyle affects β, diet affects α	$a + b_1 M + b_2 L + b_3 D + b_4 (M \times L)$
Diet affects β, lifestyle affects α	$a + b_1 M + b_2 L + b_3 D + b_5 (M \times D)$
Lifestyle and diet affect β	$a + b_1 M + b_2 L + b_3 D + b_4 (M \times L) + b_5 (M \times D)$

M, individual mass (in the first case) or colony mass (in the second case); L, lifestyle; D, diet; α, scaling intercept; β, scaling exponent. All models assumed continuous variables in $\log_{10}$ scale.

Statistical analyses

We used a linear model with $\log_{10}$-transformed variables to determine the scalings of individual metabolic rate with individual mass ($n = 63$), and of individual mass with colony mass ($n = 44$). In both cases, we considered all possible alternative models, including lifestyle and/or diet as covariates, both as independent effects and/or in interaction with the continuous predictor, to test for their effect on the scaling (Table 1). Further, we considered two versions of each model: with and without phylogenetic autocorrelation structure (see later). A similar approach was used to test for effects of lifestyle and diet on colony mass ($n = 44$), except that their interaction was not considered (all sedentary species were wood feeders, which prevented estimating the interaction term). For each dependent variable, alternative models were ranked according to Akaike's information criterion corrected for sample size (AICc), and the model with the lowest AICc value (with a difference of at least two units to the next model) was judged the most supported one (Burnham & Anderson, 2002). If one or more models were within two AICc units from that with the lowest value, we interpreted the model with fewest parameters to avoid spurious inferences (Arnold, 2010).

The phylogenetic variant of each model assumed a residual autocorrelation structure based on Pagel's λ (Freckleton *et al.*, 2002). Pagel's λ typically varies from 0 to 1, with the former meaning independence between trait and phylogeny, and the latter implying perfect correlation between trait divergence and phylogenetic relatedness (under Brownian evolution). Phylogenetic relations were inferred from a well-supported, family-level tree (Bourguignon *et al.*, 2015), complemented with other studies for resolving lower-level interrelations (Fig. 1, File S1). Whenever relationships within a clade could not be completely determined from the literature, they were treated as polytomies. As most species lacked published, comparable molecular data to allow branch length estimation, we assumed uniform branch lengths, which nonetheless have been shown to retain most phylogenetic information (Freckleton *et al.*, 2002).

For each dependent variable, confidence intervals (95% CI) were computed for all coefficients of the best-ranked model. When this model included an interaction, the scaling exponent of each covariate state (e.g. soil feeder or wood feeder) was obtained by summing the coefficient of the continuous predictor with the interaction term while specifying the respective covariate state in binary code (e.g. soil feeder = 0 and wood feeder = 1). Confidence intervals for such exponents were obtained by fitting the model twice, each time with a different baseline (i.e. different categorical state coded as 0) (Figueiras *et al.*, 1998). This approach was also used for computing the confidence interval for the intercept of each covariate state. Confidence intervals of scaling exponents were used to test whether they were consistent with theoretical expectations (i.e. whether they included 0.67 and/or 1). All models were fitted using generalised least squares. Analyses were run in R 3.2.3 (R Core Development Team 2015), with support of packages 'MuMIn' (Barton, 2016) and 'ape' (Paradis *et al.*, 2004).

Results

Of the 100 species included in our sample, 20 species were classified as sedentary, whereas 80 species were classified as foragers. All sedentary species were wood feeders. In contrast, among forager species, 40 species were wood feeders and another 40 species were soil feeders. Individual mass spanned three orders of magnitude, ranging from 0.5 mg in *Microtermes* sp. to 70.7 mg in *Zootermopsis angusticollis* Hagen. Colony mass spanned six orders of magnitude, ranging from 0.33 g in *Cryptotermes brevis* Walker to 19 375.67 g in *Macrotermes subhyalinus* Rambur.

In all analyses, there was clear support for a single model over the alternatives, with the difference in AICc between the best and second best models always higher than two (Table 2; Tables S3–S5 in File S1). Moreover, all best-ranked models included phylogenetic signal (i.e. $\lambda > 0.7$ in all cases) (Table 2), indicating that accounting for shared ancestry was relevant for making valid inferences about all studied relationships.

Individual metabolic rate was a function of individual mass, diet and their interaction, indicating that the scaling of individual metabolic rate with individual mass changed between diets (Table 2, Fig. 2). The intercepts of soil feeders ($\alpha = -0.53$, 95% CI: -0.81 to -0.26) and wood feeders ($\alpha = -0.55$, obtained by summing the intercept with the diet coefficient ; 95% CI: -0.83 to -0.28) were statistically indistinguishable, given the wide overlap in their confidence intervals. However, in soil feeders, individual metabolic rate scaled with individual mass to the 0.60 power (95% CI: 0.43–0.78), which was statistically indistinguishable from 0.67, but differed significantly from 1. Conversely, in wood feeders, individual metabolic rate scaled with individual mass to the 1.02 power (95% CI: 0.85–1.19), which differed significantly from 0.67 but was statistically indistinguishable from 1.

Individual mass scaled with colony mass according to an exponent of 0.25 (95% CI: 0.14–0.35), but there was a grade shift
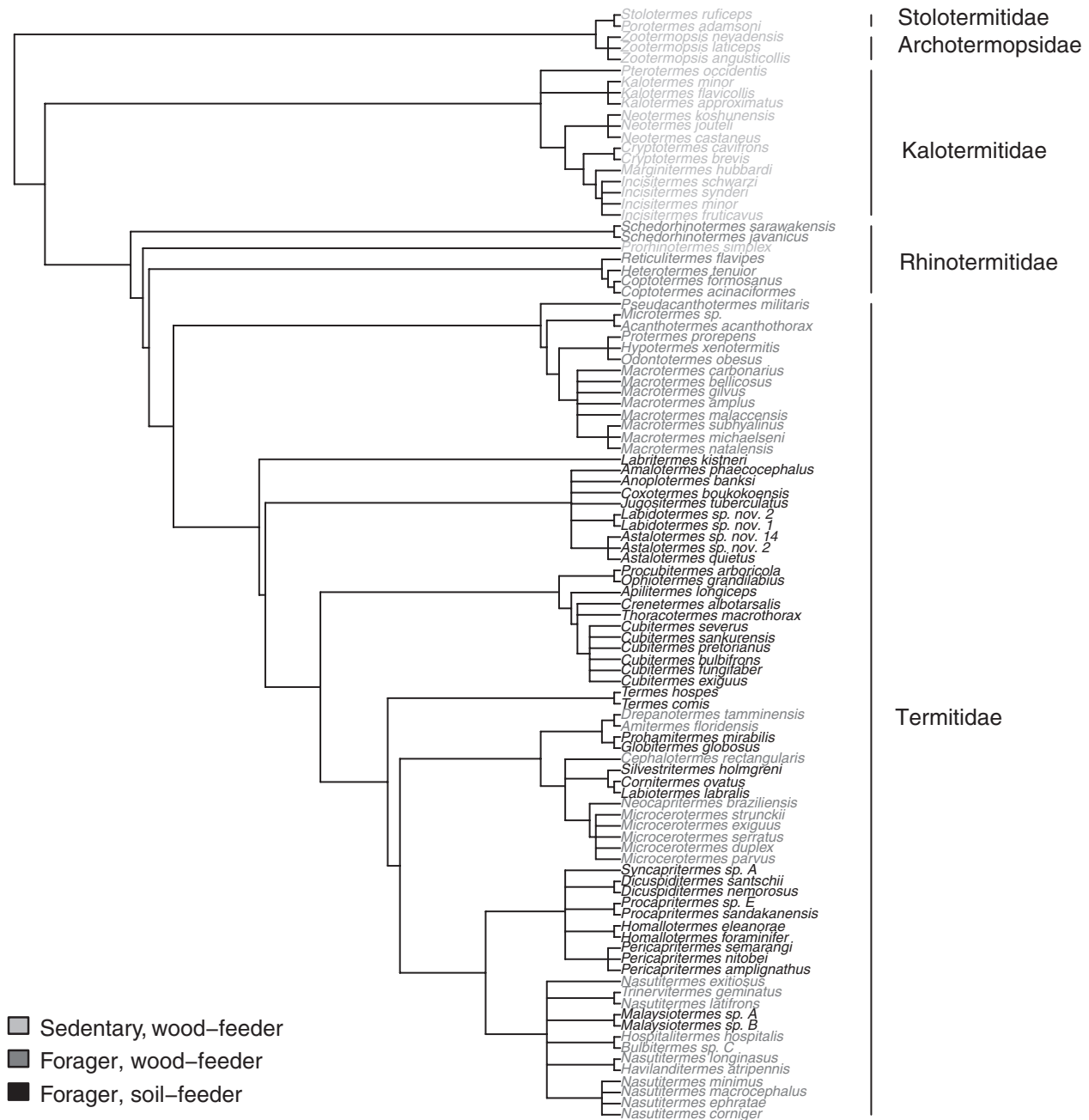
Fig. 1. Phylogeny of termite species analysed in this study, classified according to lifestyle (sedentary or forager) and diet (wood- or soil feeder). Species names were revised according to Krishna *et al.* (2013) and updated, as necessary; morphospecies names were kept as in the original publications. Branch lengths are arbitrary.

between lifestyles: the intercept decreased from sedentary to forager species (Table 2, Fig. 3). Sedentary species averaged 24.6 ± 22.73 mg (mean $\pm$ SD) in individual mass, whereas forager species averaged 4.94 ± 3.25 mg. This grade shift was also related to an increase in colony mass from sedentary to forager species: sedentary species averaged 51.23 ± 87.83 g in colony mass, whereas forager species averaged 1705.85 ± 4052.63 g (Table 2, Fig. 4).

Discussion

Our study produced two main findings. First, individual metabolic rate scaled with different exponents in soil feeders and wood feeders. This contradicts suggestions that colonial organisms comply to a single, universal β, as often claimed for unitary organisms (Riveros & Enquist, 2011; Shik *et al.*, 2012), and may partly explain why previous assessments of

Table 2. Best-ranked models of metabolic and life history scalings in termites.

Response	ΔAICc	R^2	λ	Predictor	Coefficient (95% CI)
Metabolic rate	2.12	0.81	0.77	Intercept	−0.53 (−0.81 to −0.26)
				Individual mass	0.60 (0.43−0.78)
				Diet	−0.02 (−0.19 to 0.16)
				Interaction	0.42 (0.17−0.67)
Individual mass	4.66	0.60	0.74	Intercept	−0.08 (−0.56 to 0.40)
				Colony mass	0.25 (0.14−0.35)
				Lifestyle	1.05 (0.60−1.50)
Colony mass	3.44*	0.27	0.85	Intercept	2.97 (1.76−4.18)
				Lifestyle	−1.64 (−3.00 to −0.28)

The difference between the best and next best model in terms of Akaike's information criterion (ΔAICc) is given. Models were fitted with generalised least squares, accounting for phylogenetic autocorrelation with Pagel's λ. Continuous variables (i.e. metabolic rate, individual mass and colony mass) were log_{10}-transformed. Coefficients for lifestyle and diet assume forager and soil-feeding termites as baselines, respectively.
∗Difference to the third best model; the second best model was undistinguishable from the first one (ΔAICc = 0.08), but it included a further parameter (Table S5 in File S1) and was thus judged less parsimonious (see Arnold, 2010).
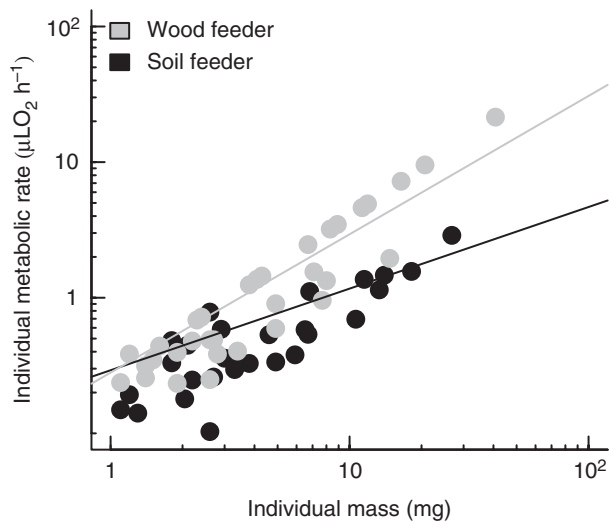

Fig. 2. Scaling of metabolic rate with individual mass across termite species. Points represent species averages ($n = 63$). Lines represent best regression fits (see Table 1).

Fig. 3. Scaling of individual mass with colony mass across termite species. Points represent species averages ($n = 44$). Lines represent best regression fits (see Table 1).

termite metabolic scaling produced conflicting results (Wood & Sands, 1978; Wheeler *et al.*, 1996; Bignell *et al.*, 1997; Jeeva *et al.*, 1999; Riveros & Enquist, 2011). Beyond this, previous inconsistencies may also reflect relatively small sample sizes, biased taxonomic coverage, or a combination thereof. Second, we revealed a nested, contradictory pattern in termite size: while individual mass increased with colony mass within lifestyles, the opposite occured between lifestyles. Overall, our analyses show that ecological traits have shaped metabolic and life-history scalings throughout termite evolution. Thus, energetic considerations on colonial life should account for niche diversification within clades.

The finding that the exponent of individual-level metabolic scaling differed between feeding groups, but not the elevation, only partly supports the MLBH. First, contrary to current suggestions (Killen *et al.*, 2010; Glazier, 2014), we found no evidence of a lifestyle effect on metabolic scaling. Second, we
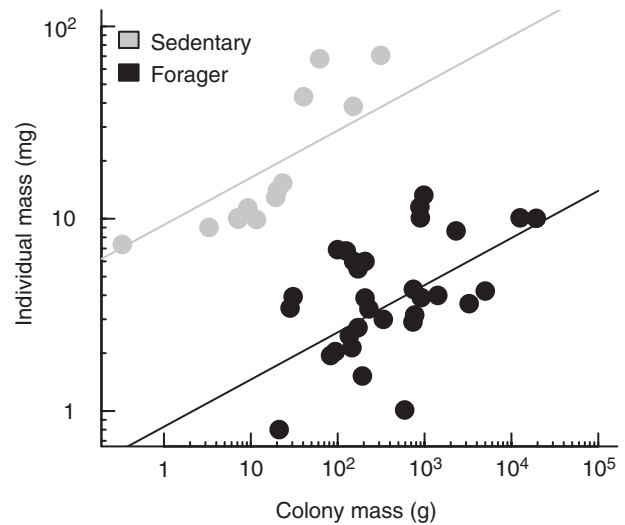
found that $\beta = 1.02$ for wood feeders and 0.60 for soil feeders, which is consistent with the prediction that soil feeders should have a lower scaling exponent than wood feeders, assuming that the former have a higher metabolic level given their relatively larger guts (Bignell & Eggleton, 1995). Under resting conditions, the MLBH predicts that a relatively high α in soil feeders should render their metabolism mainly limited by fluxes of energy and materials through body surfaces (i.e. β should tend towards 0.67), whereas a relatively low α in wood feeders should render their metabolism primarily limited by maintenance costs of volume-filling tissues (i.e. β should tend towards 1). Indeed, scaling exponents estimated for wood and soil feeders were statistically indistinguishable from 1 and 0.67, respectively. However, there was no statistical difference in α between feeding groups, despite the evidence for higher metabolic rates in species with relatively larger guts (Williams *et al.*, 2010; Naya *et al.*, 2013; White & Kearney, 2013).
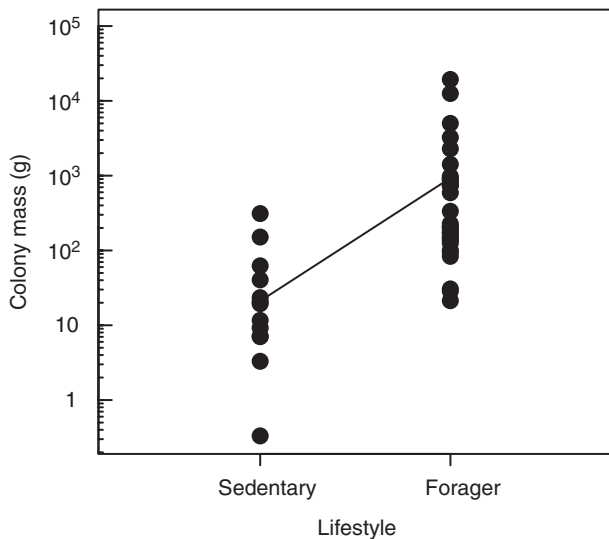
Fig. 4. Relationship between colony mass and lifestyle across termite species. Points represent species averages ($n = 44$). The line represents the best model fit (see Table 1).

A causal basis for this relationship is supported by experiments with mice, in which lineages artificially selected for increased metabolic rate also evolved relatively larger visceral organs (Książek *et al.*, 2004). Thus, while scaling exponents of soil and wood feeders are consistent with expectations based on their diets, the mechanism implied by the MLBH – a difference in metabolic level – could not be shown, suggesting that a different one may be involved.

For instance, the cell-size model (Kozłowski *et al.*, 2003; Chown *et al.*, 2007) predicts a range for β similar to that predicted by the MLBH, but ascribes it to changes in the relative contributions of cell size and cell number to body size: when changes in body size reflect purely changes in cell size, β should be 0.67; conversely, when changes in body size reflect solely variation in cell number, β should be 1. Thus, the different metabolic scalings between termite feeding groups might reflect difference in such contributions, although we cannot determine this at this time. Alternatively, consumer-resource models predict feeding rates to scale sublinearly ($\beta < 1$) with body mass in organisms that forage in two dimensions (e.g. land or benthonic surface) and approximately linearly ($\beta \approx 1$) in organisms that forage in three dimensions (e.g. open air or water), ranging from 0.58 to 1.06 (McGill & Mittelbach, 2006; Pawar *et al.*, 2012). While such models assume rather than predict a given metabolic scaling, feeding rates should at least partly reflect metabolic rates if organisms are to meet their energetic demands (Rall *et al.*, 2012; Twomey *et al.*, 2012). Interestingly, the metabolic scaling exponents estimated for soil feeders (which forage mainly close to the soil organic horizon, i.e. in two dimensions) and wood feeders (which often forage throughout vegetation strata, i.e. in three dimensions) match these boundaries very closely ($\beta = 0.60$ and 1.02, respectively), suggesting that their difference might reflect the dimensionality of their foraging space. However, data on termite feeding rates are too sparse to address this possibility at this time.

In agreement with our prediction, individual mass increased with colony mass. This relationship is important for colonial metabolism because larger individuals often have relatively lower metabolic rates; if colony metabolism equals the summed metabolism of individuals, a positive scaling of individual mass with colony mass implies that larger colonies will also necessarily have relatively lower metabolic rates (Waters, 2014). Accordingly, colony-level metabolic scaling of ants could be predicted solely from the scalings of individual mass with colony mass, and of individual metabolic rate with individual mass (Shik *et al.*, 2012). In this light, our results suggest that colony-level negative allometry in metabolic scaling is more likely to apply to soil feeders than to wood feeders, as the latter showed isometric scaling of individual metabolic rates. In line with this, whole-colony metabolic scaling of fungus-farming ants has been shown to differ between farming strategies (Shik *et al.*, 2014). There are, however, other factors that could affect whole-colony metabolic scaling independently of average individual mass, such as the colony-level scalings of body size distribution or activity level (Waters, 2014).

The grade shift between lifestyles in the scaling of individual mass with colony mass supports the hypothesis that the transition between sedentary and forager termites changed the selective regime to which termites were subject (Roisin, 2006; Rupf & Roisin, 2008; Roisin & Korb, 2011). Sedentary termites are prone to depletion of their nesting food source and, thus, keep high developmental plasticity as pseudergates, which can moult into alates and disperse under high starvation risk. In contrast, forager termites can explore a wider range of resource patches, thus decreasing starvation risk, on the one hand, and selecting for enhanced foraging efficiency on the other. Foraging efficiency can be increased by making individual foragers more efficient, more numerous, or both (Dornhaus *et al.*, 2012). A larger workforce in turn is most easily achieved by decreasing body size, as the same resource input can be allocated to more individuals (Bourke, 1999; Nalepa, 2011). Accordingly, forager termites have evolved large populations of small-bodied, specialised workers. Thus, the grade shift between lifestyles is consistent with a trade-off in resource allocation where selection for larger colonies in forager termites favoured smaller individuals as a correlated response (Bourke, 1999; Nalepa, 2011).

Overall, our results reveal contradictory evolutionary trends in termite size: while individual mass increases with colony mass within lifestyles, the opposite occurs between lifestyles. Individual mass also increases with colony mass in ants (Geraghty *et al.*, 2007; King, 2010; Shik *et al.*, 2012), suggesting that this pattern might be a common outcome of colonial evolution. Yet, sociobiological models typically assume a trade-off in social resource allocation, with larger societies arising from increased investment in individual number over size (Jaffe & Deneubourg, 1992; Karsai & Wenzel, 1998; Bourke, 1999; Nalepa, 2011; van Oudenhove *et al.*, 2013; Feinerman & Traniello, 2015). While the pattern we found between termite lifestyles agrees with this, the pattern within them (together with that reported for ants) clearly does not. Alternatively, Tschinkel (1991) hypothesised that body size and colony size should increase together, given that larger individuals live longer, thus decreasing individual turnover rate. Accordingly, simulations based on the model ant

Solenopsis invicta Buren showed that the two main endogenous traits regulating colony size are queen reproductive rate and worker longevity (Asano & Cassill, 2011), both of which increase with body size across ant species (Shik *et al.*, 2012). We suggest that this mechanism may also account for the pattern observed within termite lifestyles. Yet, individual mass scaled with colony mass with a significantly lower exponent in termites (0.25; 95% CI: 0.14–0.35) than in ants (0.47; 95% CI: 0.37–0.57) (Shik *et al.*, 2012). No current hypothesis predicts the specific exponent of this relationship or how it should vary, and this is an interesting venue for further research.

As with all interspecific scaling analyses, ours has some caveats. First, assigning variation in scaling relationships to particular traits is complicated by correlations between niche traits. For instance, all sedentary species are also wood feeders. Perhaps there are more subtle differences in individual-level metabolic scaling between wood and soil feeders within forager species (Fig. 2). Second, a trait's effect may be confounded by its phylogenetic distribution. For instance, forager termites have evolved independently at least three times (Roisin & Korb, 2011), but for some of these origins (e.g. Hodotermitidae), there are no comprehensive data on the variables analysed here. Third, colony mass can vary substantially within species, and thus using species averages is a rough approximation (Mason *et al.*, 2015). Unfortunately, comprehensive intraspecific data on the variables of interest are scant, and using species averages is the best option currently available (e.g. Hou *et al.*, 2010; Shik *et al.*, 2012). Resolving these issues will require more, relevant data, and our results should be viewed with such limitations in mind. Despite this, they make clear that diversification in traits other than size has left permanent signatures in fundamental scaling relationships of termites.

Metabolic scaling is a key property of organisms, and there is increasing evidence that it can be affected by ecological factors (Glazier, 2005, 2010, 2014; McNab, 2007; Killen *et al.*, 2010). However, only recently, the metabolic underpinnings of colonial life have been explicitly considered, even though colonial organisms are often ecologically dominant. Using a comparative dataset assembled from the literature, we provide evidence that ecological factors also shape metabolic and life-history scalings in termites, a major lineage of social insects. First, individual metabolic rate scaled hypometrically in soil feeders, but isometrically in wood feeders, consistent with expectations derived from the MLBH. However, there was no difference in scaling elevation between feeding groups, suggesting a mechanism other than that proposed by the MLBH. More generally, the difference between feeding groups contrasts with suggestions of a single, universal exponent of metabolic scaling (Hou *et al.*, 2010; Shik *et al.*, 2012). Second, we uncovered a neglected, nested pattern in termite evolution: the transition from the sedentary to the forager lifestyle resulted in larger colony size at the expense of individual size, whereas within lifestyles, species with larger colonies tend to have larger individuals. The latter contradicts the negative relationship often posited by sociobiological models. Our results concur with Tschinkel (1991) that we have been 'missing critical relationships', thus running the risk of 'devising unrealistic schemes of social insect evolution'. We suggest that scaling considerations on the evolution of colony-living should account for the natural diversity of such relationships, as revealed here.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12362

Table S1. Raw data on individual-level scaling of metabolic rate.

Table S2. Raw data on colony-level scaling of individual mass.

File S1. Details on the comparative dataset, and Tables S3–S5 and Figure S1.

Table S3. Information-theoretic evaluation of remaining models on the interspecific scaling of individual metabolic rate with individual mass in termites.

Table S4. Information-theoretic evaluation of remaining models on the interspecific scaling of individual mass with colony mass in termites.

Table S5. Information-theoretic evaluation of remaining models on the effects of lifestyle and diet on species colony mass in termites.

Figure S1. Sensitivity analysis of interspecific scaling of individual metabolic rate with individual mass in termites.

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