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Letter to Editor

Disentangling the relative contributions of variables determining the divergence of hoarding strategies of rodents

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Understanding the driving mechanism of the divergence of hoarding strategies of animals (i.e., scatter-hoarding vs. larder-hoarding) is crucial to understand the ecological and evolutionary implications of plant–animal interactions. Zhang et al. (2022) compiled a global-scale dataset from the published literature including 183 species of seed-hoarding rodents, and concluded that phylogenetic conservatism, functional traits, and environmental factors counted for the hoarding behavior divergence of rodents. A more thought-provoking question may be asked: Do these variables contribute equally or not to explain the divergence of hoarding strategies? Here, we re-analyzed Zhang et al.'s (2022) dataset using partial R^2_{lik} calculation (Ives 2019) to parse out the relative contributions of these variables. It is a challenge to disentangle the variance explained by each variable when the model includes covariances, such as phylogenetic signal. Recently, partial R^2_{lik}, raised by Ives (2019) makes it possible to compare the relative contributions of fixed variables and covariances. The partial R^2_{lik} for each variable was calculated by comparing the full model with a reduced model in which the focusing variable was removed from the full model, and measuring the reduction in explained variance (function *R2.lik* in package "rr2", Ives and Li 2018; Ives 2019). The full model was a phylogenetic logistic regression that assumed an Ornstein–Uhlenbeck evolutionary model (Ives and Garland 2010), with hoarding strategy (scatter-hoarding vs. larder-hoarding) as dependent variable, phylogeny as covariances, and body mass (log-transformed), brain mass, EQ (Encephalisation quotient, the ratio between observed and expected brain mass), diet type (plant seed vs. omnivore), and AML (absolute median latitude of distribution) as independent variables (function *phyloglm* in package "phylolm", Tung Ho and Ané 2014). Here, only the "categorical hoarding dataset" in Zhang et al. (2022) was used which included 109 rodent species with a clear hoarding strategy, while the "continuum hoarding dataset" was not analyzed because of the small sample size. The mammal phylogeny by Upham et al. (2019) was used in this study, and 100 trees were randomly selected to reduce the potential influences of phylogenetic uncertainty. The average partial R^2_{lik} values based on the 100 randomly selected phylogenetic trees were reported (Table 1, Figure 1).

Phylogenetic conservatism is one of the most important variables explaining hoarding strategy divergence (partial R^2_{lik} = 19.62%) (Figure 1). While in the model with phylogeny alone, the partial R^2_{lik} increased to 49.01% (full-model PHY, Table 1). Partial R^2 calculation provides a way to compare measured and unmeasured traits whose effects are captured by phylogeny conservatism (Ives 2019; Wang et al. 2022); therefore, the partial R^2_{lik} associated with the phylogeny will reflect the partial R^2_{lik} of latent traits that themselves have phylogenetic signals. In the full-model PHY, although diet type and EQ were not included, their effects on hoarding strategy divergence would still be reflected by the partial R^2_{lik} of phylogeny. In other words, "Phylogeny" is acting as a surrogate for the component of latent variables that has a phylogenetic signal.

Both EQ and diet type explained a considerable amount of divergence of hoarding strategies (Table 1, Figure 1). Diet type showed a strong phylogenetic signal (a value = 0.03), and we may argue that the strong effects of diet type on hoarding strategy divergence is mainly because of the phylogenetic conservatism of both diet type and hoarding strategy divergence. The same explanation also applies to EQ which also shows a modest phylogenetic conservatism (Pagel's λ value = 0.37). However, the reduction in the explained variance of the full model which concluded all the 6 variables was similar when dropping diet type or EQ compared with dropping phylogeny alone (17.35% vs. 19.62% and 18.59 % vs. 19.62%, respectively) (Figure 1), indicating that regardless of evolutionary history, both diet type and EQ always play important roles in shaping the divergence of hoarding strategy. While for body mass, brain mass, and AML, the models always showed very

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Table 1. Partial contribution of each variable (body mass, brain mass, EQ [Encephalization quotient, the ratio between observed and expected brain mass], diet type (granivore vs. omnivore), AML [absolute median latitude of distribution], and phylogenetic conservatism) to the variation in hoarding behavior divergence among the 109 rodent species

Full model	Reduced model	R^2_{lik} (%)	ΔlogLik	*P*-value
PHY+EQ+Diet+Body+Brain+AML	EQ+Diet+Body+Brain+AML	19.62	6.79	< 0.001
PHY+**EQ**+Diet+Body+Brain+AML	PHY+Diet+Body+Brain+AML	18.59	6.43	0.003
PHY+EQ+**Diet**+Body+Brain+AML	PHY+EQ+ Body+Brain+AML	17.35	5.90	0.001
PHY+EQ+Diet+**Body**+Brain+AML	PHY+EQ+Diet+ Brain+AML	3.61	1.14	0.287
PHY+EQ+Diet+Body+**Brain**+AML	PHY+EQ+Diet+Body+ AML	2.16	0.68	0.329
PHY+EQ+Diet+Body+Brain+**AML**	PHY+EQ+Diet+Body+Brain	-2.66	-0.76	0.845
Phylogenetic conservatism (PHY)	1	49.01	25.55	< 0.001
Encephalization quotient (EQ)	1	25.07	15.73	< 0.001
Diet type (Diet)	1	26.10	16.48	< 0.001
Body mass (Body)	1	0.10	0.06	0.738
Brain mass (Brain)	1	2.03	1.12	0.135
Absolute median latitude of distribution (AML)	1	2.70	1.49	0.084

The partial R^2_{lik} value for each variable was calculated by comparing the full model with a reduced model in which the focusing variable (in bold) was removed from the full model. The values of ΔlogLik were the changes in log-likelihood after removing the focusing variable.

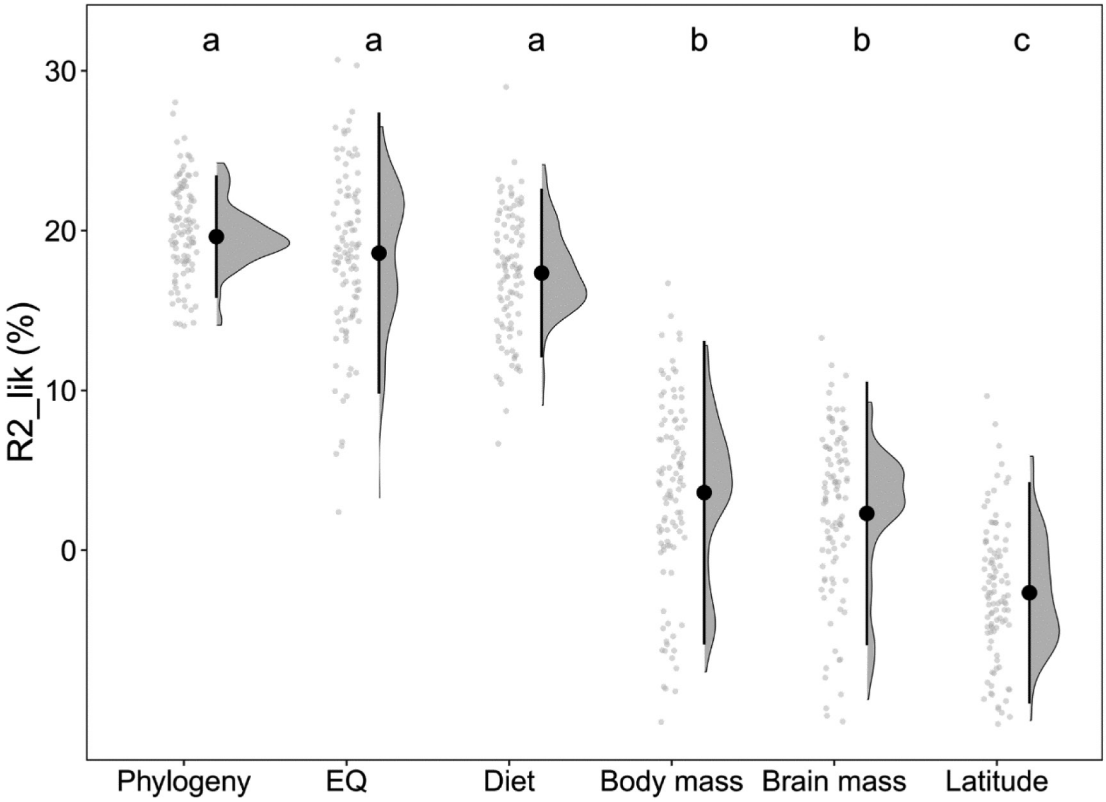

Figure 1. The relative contributions of different variables to the variation in hoarding behavior divergence of rodents. The partial R^2_{lik} values were based on the 100 randomly selected phylogenetic trees, and the differences among variables were estimated by the Kruskal–Wallis test followed by a Nemenyi test. Bars in the violins are standard deviations. Different letters indicate significant differences among variables ($P < 0.01$).

small partial R^2_{lik} values no matter if phylogeny, EQ and diet type were included or not (Table 1), suggesting that these variables are irrelevant to explain the interspecific variation in hoarding strategy.

Our results highlighted the equal contributions of phylogenetic conservatism, EQ, and diet type in shaping the divergence of rodents' hoarding strategy. Many functional traits, in both animals and plants, are influenced by both phylogeny and other predictor variables (Li et al. 2020; Heldstab et al. 2022); however, few studies disentangled their relative contributions (but see Wang et al. 2022). The calculation of phylogenetic partial R^2 is an effective way to compare the relative contributions of multiple variables and phylogeny on a given trait. Therefore, we call for future studies to take this into account, which may help us better understand the ecological and evolutionary patterns of functional traits.

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Author contributions

BW conceived the ideas, designed methodology, analyzed the data, and write the manuscript.

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