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# Hungry for nutrients in heterogeneous environments: Nutrient temporal variance and covariance effects on the performance of nutritionally co-limited individuals.

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## Abstract

Consumers face the challenge of satisfying their demands for nutrients with the supply of those nutrients in the environment. Yet, nutrient supply is highly variable at the spatiotemporal scales experienced by individuals. Because physiological performance traits are saturating functions of nutrient supply, long-term individual performance is generally negatively affected when consumers experience dietary variability in the supply of single limiting nutrients (Jensen's inequality). However, consumers can also be co-limited by multiple nutrients. Yet the long-term effect of dietary variability in co-limited consumers remains poorly studied. Here, we use phosphorus and cholesterol co-limited *Daphnia magna* as experimental model for investigating how variance in each nutrient as well as their covariance affect the consumers' long-term somatic growth across different variance frequencies (high: 1cycle/12h, intermediate:1cycle/24h, low:1cycle/48h) and sequences (starting with low or high nutrients). For single nutrients, we find that growth rate decreases with decreasing environmental frequencies at a rate which strongly depends on the temporal sequence. For nutrient co-limitation, growth rate decreases occur only at high and low frequencies and are strongly dependent on the covariance of the co-limiting nutrients. Interestingly, we find that covariance acts in opposite directions at the two extreme frequencies. In a second step, we use DEB-modeling to show how the digestive trade-offs, the nutrient reserves and the biomass synthesizing-unit can explain our experimental observations and derive general predictions. Our work provides a framework for understanding how the spatiotemporal structure of nutritionally complex landscapes constraint individual performance and can therefore influence foraging behavior, dietary strategies and physiological adaptations.

**Keywords:** Daphnia, Dietary mixing, Dynamic energy budget theory, Food quality, Herbivore, plant interactions, Integrative growth, Nonlinearity, Phosphorus limitation, Scale transition approaches, Sterol limitation

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