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NEWS AND VIEWS

PERSPECTIVE

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Intrapopulation variance in ecophysiological responses to water limitation in a butterfly metapopulation suggests adaptive resilience to environmental variability

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How organisms that are part of the same trophic network respond to environmental variability over small spatial scales has been studied in a multitude of systems. Prevailing theory suggests a large role for plasticity in key traits among interacting species that allows matching of life cycles or life-history traits across environmental gradients, for instance insects tracking host-plant phenology across variable environments (Posledovich et al. 2018). A key aspect that remains understudied is the extent of intrapopulation variability in plasticity and whether stressful conditions canalize plasticity to an optimal level, or alternatively if variation in plasticity indeed could increase fitness in itself via alternative strategies. In a From the Cover article in this issue of *Molecular Ecology*, Kahilainen et al. (2022) investigate this issue in a classical insect study system, the metapopulation of the Glanville fritillary butterfly (*Melitea cinxia*) in the Åland archipelago of Finland. The authors first establish how a key host plant responds to water limitation, then quantify among-family variation in larval growth and development across control and water-limited host plants. Finally, they use RNA sequencing to gain mechanistic insights into some of these among-family differences in larval performance in response to host-plant variation, finding results suggesting the existence of heritable, intrapopulation variability in ecologically relevant plasticity. This final step represents a critically important and often overlooked component of efforts to predict sensitivity of biological systems to changing environmental conditions, since it provides a key metric of adaptive resilience present in the system.

KEYWORDS
climate change, phenotypic plasticity, population dynamics, water limitation

Predicting how environmental variability will affect trophic interactions is not straightforward, since effects can differ between interacting species (van Asch & Visser, 2007). One trophic interaction that is both globally ubiquitous and especially susceptible to climatic variability is between insect herbivores and their host plants, since major environmental variables (e.g., temperature or water availability) affect both trophic levels. Even though theory predicts large roles for plasticity in life-history traits in mediating environmental variability on host-plant quality, few studies have undertaken rigorous investigation at both he host as well as herbivore level. An important exception is a study on *Sitobion avenae* aphids from northern China, which reported that the contribution of clonal variability within each population to performance was greater than among-population variability (Dai et al., 2015). This strongly suggests further studies exploring intrapopulation variability in plasticity to host quality are warranted.

In the current paper, Kahilainen et al. explore these questions using a model system of evolutionary ecology—the Glanville fritillary butterfly (*Melitaea cinxia*) (Figure 1). The authors describe both canalized and divergent responses to water limitation in the host plants, specifically so that amino acids and aromatic compounds seemed to increase in most plants as a consequence of water limitation, while carbohydrates, and the iridoid glycosides aucubin and catalpol were mixed. Butterfly larvae reared using a controlled family design on control or water-limited plants also showed divergent responses. Importantly, whereas larvae of four butterfly families grew larger, developed faster and/or had lower overwintering mortality when feeding on water-limited host plants during early larval developmental stages, the opposite was true for three of the families, and mixed responses were observed in two families. These life-history responses were matched on a physiological level, as transcriptomic patterns were parallel to the divergent developmental responses. These findings allowed the authors to match the between-family transcriptomic differences with the divergent phenotypic responses, potentially due to differences in metabolizing amino acids, nutrient storage and intracellular transport. Thus, the insects' life-history and physiology patterns were shown to be causally coherent and consistent with the observed water limitation-induced changes in plant physiology.

The present study demonstrates that water limitation not only led to varying degrees of stress, which would be expected, but that it actually led to higher performance in some of the insect families compared to controls (Figure 2). This could indicate, intriguingly, that some of the insect families might have optimized their feeding physiology to capitalize on the changes that water limitation brings about in the host. Since the system is found in open meadows that regularly experience water limitation, it can be assumed that different feeding physiologies could be optimal in different years and patches. We are excited by these findings since they suggest segregating alternative strategies of plastic responses in these herbivores. If the results hold also for a larger sampling, a mechanism of major ecological significance will be revealed. Therefore, a larger study is warranted. Importantly, it is also necessary to substantiate these suggestive patterns, with greater sampling among families, a design minimizing batch rearing effects, and additional physiological data that can test RNA sequencing-based hypotheses. Additionally, we think there is much to be gained by incorporating a full-sib or family-level design for the plant side of these interactions (Figure 2), as such variation could be part of the explanation for variable plant stress responses in carbohydrate and iridoid glycoside levels. However, firmly establishing the role of intrapopulation levels of plasticity among interacting trophic levels is challenging. This is because there is a tradeoff in research effort, as studying both levels (e.g., plant and insect) at the same time results in far too many pairwise interactions. One approach has been to hold one level constant, while looking across family groups (e.g., Nallu et al., 2018). Another is suggested by this study. By surveying roughly 10 different families, variation among them was identified. Such effort could be done at both trophic levels (Figure 2), allowing for the possible alternative strategies to be identified, and then the interaction between those studied in more detail.

In sum, while few studies have investigated both sides of the plant–insect interaction, the findings by Kahilainen et al. strongly

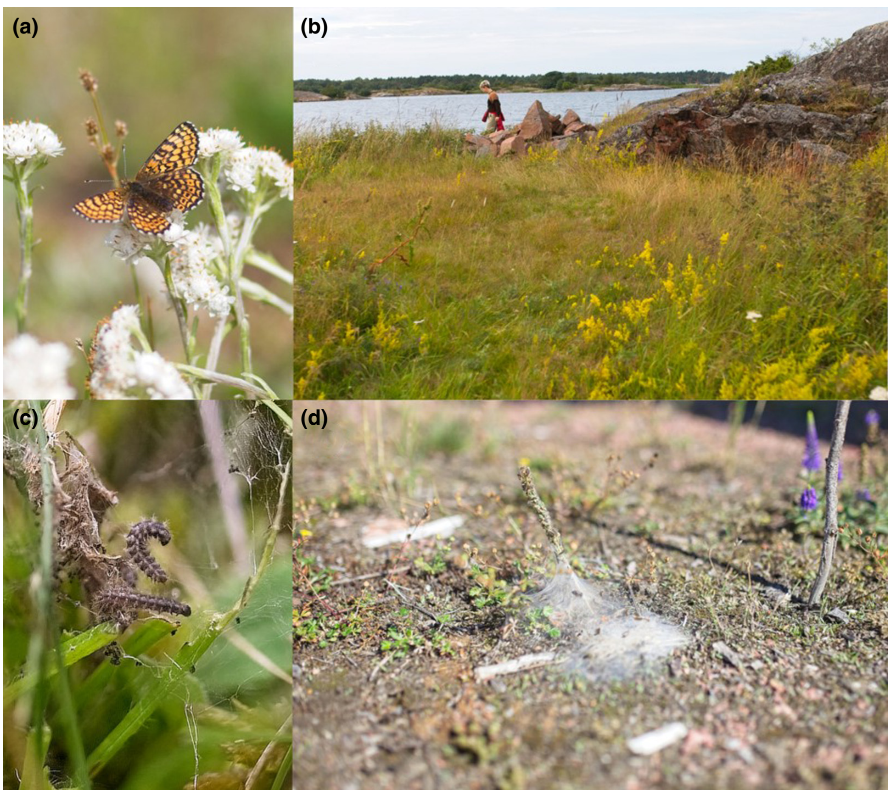

FIGURE 1 In the Åland islands of Finland, the Glanville fritillary butterfly (a) inhabits dry meadows (b). The gregarious full-sib larval groups are typically limited to a single or few host plant individuals (c) on which they also overwinter inside conspicuous overwintering nests (d). Due to shallow soil the habitat meadows and host plants are susceptible to periods of drought, which alters host plant quality and affects development of the larvae (photos: Aapo Kahilainen).

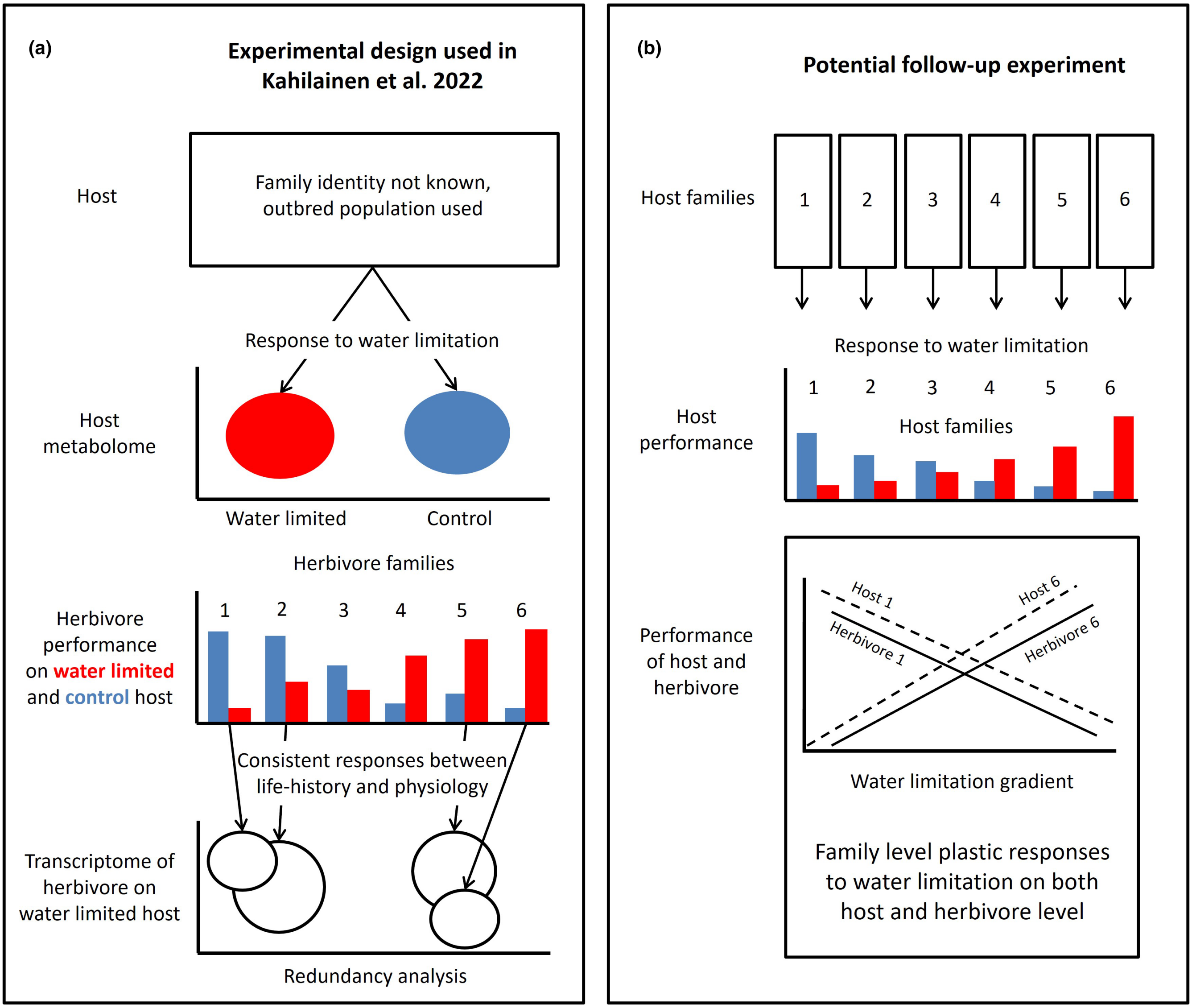

FIGURE 2 Main results and outlook. The design used in the current study by Kahilainen et al. is shown in (a) where herbivore performance on water-limited host plants led to divergence into high- and low-performing families, with responses canalized in both life-history and physiological traits. A potential expansion of the work is shown in (b) where also family-level variation in the host plant is investigated. By corearing insect and plant families that perform well in either control or water limitation treatments, researchers could factorially investigate plasticity in both partners in this trophic interaction.

suggest such efforts are warranted. Indeed, the current study reveals encouraging evidence of larger than expected variation in performance traits on very small spatial scales, which could suggest insect populations are more resilient to environmental changes than previously thought. These mechanisms need to be explored further in this and other insect–plant systems.

AUTHOR CONTRIBUTION

PL and CWW contributed equally to the writing of the paper.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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