From plants to herbivores: novel insights into the ecological and evolutionary consequences of plant variation

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Introduction

Individuals differ! This observation goes already back to Aristotle almost 2500 years ago, but individual differences are nowadays still highlighted in various areas of social and natural sciences. Almost every day, new fascinating layers of this variation, with their intriguing causes and consequences for species interactions, are discovered. Likewise, variation within and among plant individuals and across landscapes are critical for plant–herbivore interactions, but not fully explored. Micro- or macro-scale spatial heterogeneity in the abiotic and biotic environment can generate significant within- and among-plant variation (e.g., Schaeffer et al. 2018), and recent studies have provided novel insights into how plant chemistry impacts herbivores, microbes and natural enemies (Albrechtsen et al. 2018; Calf et al. 2018; Coley et al. 2018; Cuny et al. 2018). Moreover, the effects of plant chemical traits are often considered in isolation, but they may act together with other features of growth and defense to form distinct trait combinations or syndromes (Coley et al. 2018; Kergunteuil et al. 2018; Tewes and Müller 2018). Yet it is important not to just focus on plant traits, as environmental change such as habitat fragmentation and climate change also alter the relative abundances of herbivores and predators (van der Putten 2012; Genua et al. 2017).

In this special topic, stimulated by the Plant–Herbivore Interactions Gordon Conference of 2017, we invited a series of reviews and empirical studies that build on recent

advances to examine the drivers and importance of variation within and among plants at the micro- and macro-scale for the interactions among plants, herbivores and other organisms. The studies of this special topic cover a broad range of plant life forms, from marine algae in an aquatic system (Ledet et al. 2018) to terrestrial herbs (Calf et al. 2018; Chiriboga et al. 2018; Cuny et al. 2018; Howard et al. 2018; Humphrey et al. 2018; Kergunteuil et al. 2018; Quintero and Bowers 2018), to shrubs (Nell et al. 2018; Ochoa-López et al. 2018), to long-lived trees (Albrechtsen et al. 2018; Bagchi et al. 2018; Cipollini and Peterson 2018; Coley et al. 2018; Falk et al. 2018; Lämke and Unsicker 2018). In twelve case studies and four review papers, selected aspects of the huge variation in phenomena and underlying mechanisms are highlighted and new research questions opened, which may inspire further research in this exciting field. Below we highlight some of the key findings of these papers.

Drivers of plant variation

Intrinsic mechanisms underlying within- and among-plant variation

Two reviews (Coley et al. 2018; Lämke and Unsicker 2018) examine the underlying molecular mechanisms and consequences of variation in plant defenses to long-lived trees, which are often understudied. Lämke and Unsicker (2018) indicate that genome duplication, followed by functional diversification as well as hybridization are major drivers of variation. Coley et al. (2018) review and integrate their years of research on *Inga*, a speciose genus of tropical trees. They show that at an interspecific level, diversity in secondary metabolite profiles does not necessarily arise from the evolution of novel compounds, but can rather result from novel combinations of common compounds, presumably due to changes in gene regulation.

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Nell et al. (2018) use the presence of sexual dimorphism in a dioecious shrub to compare the relative impacts of sex-based and non-sex-based genetic variation on herbivores, predators and arthropod communities. They find that the effects of non-sex-based genetic variation are stronger but that both, via parallel and unique mechanisms, affect plant-associated arthropod communities.

Yet patterns of trait expression can vary in time as well. While changes that occur during leaf development are often strong (see Coley et al. 2018 for a nice overview of this topic), ontogenetic shifts are likewise important. Quintero and Bowers (2018) and Ochoa-López et al. (2018) provide new perspectives to the ecology and evolution of ontogeny. Quintero and Bowers (2018) find that over plant ontogeny, physical and chemical defenses increase, while nutritional quality decreases, and that these changes in plant ontogeny mostly affect the behavior and physiology of younger instars of an herbivore. For the herbivores, seasonal synchrony between their own and the host plant's ontogeny is crucial but may be impeded by shifts due to climate change (Coley et al. 2018; Quintero and Bowers 2018). Using siblings of several genotypes of a shrub grown in a shadehouse and in the field, Ochoa-López et al. (2018) reveal that the proportion of genetic variation in defensive traits changes as a function of plant age and type of defense, differing between trichome density and the cyanogenic potential. Ontogenetic trajectories for trichome density show high plasticity, which may constrain the evolution of this complex trait.

Extrinsic mechanisms underlying within- and among-plant variation

Plant traits are also strongly affected by the environment the plant individual faces at any point in space and time. Humphrey et al. (2018) investigate how local adaptation to certain abiotic and biotic conditions proceeds at a fine-grained spatial (micro-)scale. Performing reciprocal transplant experiments in the field and manipulating the conditions in a greenhouse experiment they provide evidence for adaptive micro-geographic divergence and for heritable differences in the response to shading. The defense phenotypes track the parental habitats, with elevated defenses in plants from open habitats where herbivore pressures are high (Humphrey et al. 2018).

In various temperate trees, temperature, water availability and herbivory are major factors causing changes in concentrations of volatile organic compounds and phenolics, as reviewed by Lämke and Unsicker (2018). In contrast to temperate trees, induction by herbivores seems to be of less relevance in expanding leaves of neotropical trees, where only phenolics slightly increase after herbivore damage (Coley et al. 2018). Thus, induction patterns are highly species- and

system-specific, vary between different compound classes and may also play different roles in different ecosystems.

Variation in plant responses are not only driven by herbivores but also by members of the third trophic level. Cuny et al. (2018) show in their field study on wild lima beans that plant compensatory responses to herbivore damage are affected by parasitoids. The parasitoids reduce herbivore feeding, which in turn reduces compensatory growth and leads to the production of more and heavier seeds earlier in the season. These results offer novel insights into the huge complexity that can drive the variation in plant–herbivore interactions.

Within the last years, it has become increasingly recognized that bacteria and fungi can also play an important role in affecting plant chemistry. Chiriboga et al. (2018) investigate the effects of two root-associated bacteria species on the growth of a root herbivore and herbivory-induced emission of a maize root volatile. The weight gain of larvae of a root–herbivore is positively affected by one bacterial strain. Moreover, a plant growth promoting strain leads to an increase of volatile production and gene expression of a relevant synthase gene (Chiriboga et al. 2018). Whether this increased volatile production enhances the attractiveness to biocontrol agents needs to be tested.

Responses of herbivores and other organisms to plant variation

Trait variation can be transient and impacts herbivores at different scales. Falk et al. (2018) show that phenolic glycoside concentrations in *Populus* peak just when highly sensitive neonates of gypsy moths emerge. Furthermore, they demonstrate that tree genotypes differ in the magnitude and duration of the peak suggesting that climate-induced changes in neonate emergence may lead to differential growth and survival of different genotypes (Falk et al. 2018). Ledet et al. (2018) also take a climate change perspective and explore the short- and long-term temperature effects on plant quality of three brown algal host species and an herbivorous amphipod. Notably, the effects vary across generations. Whereas the first filial generation (F1) is mainly affected by the diet, the F2 generation is influenced by the interaction between diet quality and temperature. Moreover, the effects are highly host plant species-specific. Thus, when predicting effects of climate change, e.g., increasing temperatures, on plant–herbivore interactions both temperature-induced changes of plant quality and direct effects of the temperature on herbivores need to be considered (Ledet et al. 2018).

Connecting to previous work demonstrating that herbivores shape intraspecific plant chemotypic diversity (Jones et al. 1991; Speed et al. 2015), Calf et al. (2018) compare the metabolic variation of glycoalkaloids between several

geographic distinct populations of a herb in relation to plant resistance towards a slug. Applying a metabolomic approach, a few steroidal glycoalkaloids could be revealed that show negative correlations with slug feeding. High chemotypic diversity can also be found in other plant taxa and may be maintained as it impedes the adaptation of herbivores (Wolf et al. 2011). Similarly, the review by Coley et al. (2018) highlights that if neighboring trees in the tropics differ in their defenses, they are unlikely to share herbivores and thus coexistence of different plant and herbivore communities is enhanced. These findings indicate that chemical diversity is likely driven by herbivore pressure.

Globalization has led to the movement of invasive species, and pre-adaptation to phytochemical patterns plays an important role in host range expansion (Agosta 2006). In a review related to this topic, Cipollini and Peterson (2018) leverage recent results from their work on the emerald ash borer which is invasive in North America. They show that similarities in phloem and volatile chemistry potentially mediated host switching of this insect to non-host species. Understanding the mechanisms underlying potential host switches may also be helpful for predicting pest outbreaks.

Whereas invasive herbivore species may broaden their dietary spectrum, reductions in dietary specialization of herbivore communities are consistently found in association with fragmented landscapes, but the causes remain poorly understood. Bagchi et al. (2018) review the bottom-up and top-down effects of fragmentation on the loss of specialists and its community-level consequences. They argue, for example, that dietary generalists may be better able to cope with changes in host quality due to inbreeding and that the top-down effects of deer browsing disproportionately disadvantage dietary specialists. Thus, studies of plant–herbivore interactions would profit from considering the landscape context in which these interactions occur.

Lastly, there has been increasing interest in the effects of chemical variation on plant–herbivore–microbe interactions (Tabata 2018), and here Albrechtsen et al. (2018) show that the composition of tree endophytic fungi is influenced by both host tree genotype and leaf beetle herbivory. It is notable that herbivory enriches fungal assemblages without relation to the plant genotype. In conclusion, the endophytic mycobiome is a highly diverse and dynamic interface that can shape plant–herbivore interactions, adding another layer of complexity.

Evolutionary feedbacks

In an eco-evolutionary approach, Howard et al. (2018) investigate the relative importance of rapid evolution and environmental changes in affecting mean plant resistance and growth phenotypes. They report on a soil transplant

experiment with plant lines over several years of succession with different herbivore pressures. Growth is strongly affected by succession, whereas plant secondary metabolism and herbivore resistance varies only little with the soil environment. They find that feeding by a specialist herbivore causes divergent patterns of resistance evolution within short time periods (Howard et al. 2018). The results highlight that selective pressures are likely to vary during community succession.

Kergunteuil et al. (2018) study the sources of variation of plant fitness traits along an elevation gradient. They measure plant functional traits of multiple species and reveal a high variation in convergence and divergence among traits conferring resistance against biotic or abiotic stresses. From an evolutionary perspective the question arises why variation exists in complex multi-trait defense strategies, which is elaborated by Kergunteuil et al. (2018) and Coley et al. (2018), applying multivariate statistical analyses. Kergunteuil et al. (2018) highlight the importance of simultaneously considering ‘niche partitioning’ and ‘environmental filtering’ to fully apprehend trait variation. Coley et al. (2018) find that different types of defenses have independent evolutionary trajectories.

In summary, the importance of plant variation to plant–herbivore interactions is well established and the papers in this series present new tools and emphasize the importance of both spatial and temporal variation, and its effects on the ecology and evolution of plant–herbivore interactions.

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