



## Surrounding vegetation mediates frequency of plant–herbivore interactions in leaf-feeders but not in other herbivore groups

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Received 16 December 2014; accepted 4 December 2015  
Available online 24 December 2015

### Abstract

The overall impact of herbivores on plant population dynamics is determined by a combination of herbivore impact on individuals and frequency of herbivore occurrence within the plant population. While the first component is well-explored, the second is much less studied and may depend both on plant individual traits and on local environmental conditions. In the present study, we focus on determinants of occurrence of damage by five herbivore functional groups to a wet meadow perennial, *Succisa pratensis*. We assess the role of plant individual traits (size and conspicuousness) and the surrounding vegetation (regarded as a proxy of local biotic and abiotic conditions) in a field study spread over several spatial (and partly temporal) scales.

Overall occurrence of damage both by invertebrate and vertebrate folivores and by the specialist folivore *Euphydryas aurinia* depended on the surrounding vegetation. The preferences to plant individual traits of the two former groups changed with the surrounding vegetation type as well. On the other hand, occurrence of stalk grazing did not vary with any of the tested factors and predispersal seed predators responded only to local inflorescence density. Herbivore damage occurrence varied most at the population scale in all five herbivore groups. The relative importance of the subpopulation scale was lower for vertebrates than for invertebrates. Temporal variation was higher in vertebrate herbivore groups.

Our results demonstrate that occurrence of damage by three important herbivore groups changed substantially on a relatively finely delimited gradient of local conditions even at the spatial scale of metres. Such spatial heterogeneity could give rise to a mosaic of different subpopulations within the plant population each with different dynamics. This would in turn substantially change the plant species' long-term persistence prospects in landscape.

### Zusammenfassung

Der Gesamteinfluss von Pflanzenfressern auf die Populationsdynamik von Pflanzen wird bestimmt durch eine Kombination von Einflüssen auf Individuen und der Häufigkeit des Auftretens von Herbivoren innerhalb der Pflanzenpopulation. Während

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die erste Komponente gut erforscht ist, wurde die zweite weit weniger untersucht und könnte sowohl von individuellen Merkmalen der Pflanzen als auch lokalen Umweltbedingungen abhängen. Wir konzentrieren uns hier auf die bestimmenden Faktoren für das Auftreten von Schäden durch fünf funktionelle Gruppen von Herbivoren an einer ausdauernden Feuchtwiesenpflanze: *Succisa pratensis*. Wir bestimmen die Rolle von individuellen Merkmalen (Pflanzengröße und Auffälligkeit) und der umgebenden Vegetation (als ein Abbild der lokalen biotischen und abiotischen Bedingungen) in einer Freilanduntersuchung, die sich über verschiedene räumliche (und teilweise zeitliche) Skalen erstreckt. Das Auftreten von Schäden durch pflanzenfressende Wirbellose und Wirbeltiere sowie durch den blattfressenden Spezialisten *Euphydryas aurinia* hing von der umgebenden Vegetation ab. Die Präferenzen für individuelle Merkmale der Pflanzen hingen bei den beiden erstgenannten Gruppen ebenfalls von der umgebenden Vegetation ab. Der Fraß an Blütenstengeln variierte mit keinem der getesteten Faktoren, und Samenfresser reagierten nur auf die lokale Blütenstandsichte. Das Auftreten von Fraßschäden variierte bei allen fünf Herbivorengruppen auf der Populationsebene am meisten. Die relative Bedeutung der Ebene der Subpopulation war bei den Wirbeltieren geringer als bei den Wirbellosen. Die zeitliche Variation war bei den Wirbeltieren höher. Unsere Ergebnisse zeigen, dass der Schadenseintritt sich bei drei wichtigen Herbivorengruppen deutlich entlang eines eng begrenzten Gradienten von lokalen Bedingungen änderte, sogar innerhalb von wenigen Metern. Solche räumliche Heterogenität könnte zur Bildung eines Mosaiks von Subpopulationen innerhalb der Pflanzenpopulation führen, von denen jede ihrer eigenen Dynamik folgt. Dies wiederum würde die Aussichten der Art auf ein langfristiges Überleben in der Landschaft erheblich verändern.

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**Keywords:** *Succisa pratensis*; *Euphydryas aurinia*; Plant–animal interaction; Spatial variation; Predispersal seed predation; Specialist herbivore; Generalist herbivore; Leaf feeders; Grazing

## Introduction

Herbivores can be one of the important drivers of plant population dynamics (e.g. Louda & Potvin 1995; Maron & Crone 2006; Brody, Price, & Waser 2007). The spectrum of herbivores the plants face is typically very broad (e.g. Ehrlén 1995; Irwin & Brody 2011; Rose, Russell, & Louda 2011) and correspondingly broad is the range of plant vital rates the herbivores directly affect (survival, growth, reproduction, germination, clonal growth). The overall impact of herbivores on plant population dynamics is determined by a combination of herbivore impact on plant individuals and frequency of herbivore occurrence within the plant population. While the first component can be studied both under experimental (e.g. Rautio et al. 2005; Ågren, Hellström, Toräng, & Ehrlén 2013) and *in situ* conditions (e.g. Kolb, Leimu, & Ehrlén 2007; Ehrlén & Münzbergová 2009), the second generally less studied component can be studied only in the field.

Herbivore occurrence is often mediated by the target plant's traits, mainly size (Brody 1997; Piqueras 1999; Ehrlén & Münzbergová 2009). Additional biotic and abiotic characteristics (such as microclimate, topography or identity of co-occurring plant species) of the site can be important drivers of herbivore occurrence too (Rand 1999; Kolb et al. 2007; Miller, Louda, Rose, & Eckberg 2009; Münzbergová & Skuhrovec 2013). Even within populations or within subpopulation patches, herbivores sometimes respond to relatively subtle differences in environmental conditions, such as amounts of available foliar nutrients (Loaiza, Jonas, & Joern 2011) or differences in host plant density and presence of alternative hosts (Östergård & Ehrlén 2005). On the one hand, there is evidence that effects of micro-site abiotic

conditions can outweigh the effect of plant individual traits (Förare & Engqvist 1996), but on the other some studies from relatively strong abiotic and biotic gradients report no effect of habitat conditions on herbivore occurrence or an effect inconsistent in time (Rose et al. 2011; von Euler, Ågren, & Ehrlén 2014).

The pattern of occurrence of herbivore damage is a result of three steps, all of which can be potentially influenced by biotic and abiotic site characteristics but also by population spatial configuration (see e.g. Zabel & Tschamntke 1998). A herbivore first needs to encounter plant species' population within the landscape. Subsequently, it needs to choose a particular patch or subpopulation within the chosen population and only after that, it is able to choose among plant individuals based on their individual traits and according to its perceptual abilities (Banks 1998). The herbivore's choice of patch may be driven also by other factors besides its attractiveness from the food consumption viewpoint. Surrounding vegetation can affect for example herbivore plant detection probability (Ågren, Fortunel, & Ehrlén 2006; Castagneyrol, Giffard, Péré, & Jactel 2013), relative palatability (Stastny & Agrawal 2014), competition from other herbivore functional groups (Giffard, Jactel, Corcket, & Barbaro 2012) or availability of larval habitats (Sjödin, Bengtsson, & Ekbohm 2008). The actual herbivore choices of focal plant species' populations are likely to differ between individual herbivore groups, because of their different perceptual abilities and mobility (vertebrates vs. invertebrates) as well as because of their different degree of dependence on focal plant species (specialists vs. generalists).

In the present study, we examined factors influencing the occurrence of five herbivore groups in a plant species,

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