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Does plant phylogenetic diversity increase invertebrate herbivory in managed grasslands?

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Abstract

Plant diversity and land-use intensity have been shown to affect invertebrate herbivory. Several hypotheses predict positive (e.g. associational susceptibility) or negative (e.g. associational resistance) relationships of herbivory with plant species richness. Also, the strength and direction of reported relationships vary greatly between studies leading to the conclusion that relationships either depend on the specific system studied or that other unconsidered factors are more important. Here, we hypothesized that plant phylogenetic diversity is a stronger predictor of invertebrate herbivory than plant species richness because it integrates additional information about the phenotypical and functional composition of communities. We assessed the community-wide invertebrate herbivory, plant species richness and phylogenetic diversity across a range of land-use intensities including a total of 145 managed grasslands in three regions in Germany. Increasing land-use intensity decreased plant species richness and phylogenetic diversity. Plant species richness did not predict invertebrate herbivory. By contrast herbivory moderately increased with increasing plant phylogenetic diversity even after accounting for the effects of region and land use. The strength of direct effects of land-use intensity and indirect effects via altered phylogenetic diversity on herbivory, however, varied among regions. Our results suggest that increasing phylogenetic diversity of plant communities increases invertebrate herbivory probably by providing higher resource diversity. Differences between regions underline the need to account for regional peculiarities when attempting to generalize land-use effects on invertebrate herbivory.

Keywords: Biodiversity Exploratories; Land use; Ecosystem process; Insects; Phylogeny

Introduction

Plant diversity and land-use intensity affect aboveground invertebrate herbivory (e.g. Gossner, Weisser, & Meyer 2014; Loranger et al. 2014; Scherber et al. 2006; Scherber,

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Heimann, Köhler, Mitschunas, & Weisser, 2010). Previous studies that focused on responses of herbivory to changes in plant species richness revealed, however, no consistent patterns: there is an approximately equal number of studies reporting either positive or negative relationships between herbivory and plant species richness (reviewed in Dinnage 2013). Several theoretical predictions can be made about the relationship between herbivory and plant species richness. For example, the associational resistance hypothesis (Tahvanainen & Root 1972) states that increasing number of plant species reduces invertebrate herbivory. This has been shown in meta-analysis approaches for crop fields (Letourneau et al. 2011) and forests (Castagneyrol, Jactel, Vacher, Brockerhoff, & Koricheva, 2014). The mechanisms behind this can be for example resource dilution effects for specialist herbivores, interaction between plants and natural enemies (Stiling, Rossi, & Cattell 2003) or chemical compound release depending on the neighboring plants (Himanen, Blande, Klemola, Pulkkinen, Heijari, & Holopainen, 2010). On the other hand, associational susceptibility predicts increased herbivory with increasing plant diversity. For example, increasing plant species richness can provide a wider array of additional nutritional resources for a higher number of herbivore species, the so-called dietary mixing hypothesis (after Bernays, Bright, Gonzalez, & Angel 1994). Several studies have shown a positive correlation between plant species richness and invertebrate (e.g. Plath, Dorn, Riedel, Barrios, & Mody, 2012; Unsicker, Oswald, Köhler, & Weisser 2008; but see Guyot, Castagneyrol, Vialatte, Deconchat, & Jactel, 2016 for negative correlation and Kambach, Kühn, Castagneyrol, & Bruelheide 2016 for no effect of plant diversity and herbivory). Studies which included additional predictors such as functional composition of plant communities found no relationships between plant species richness and herbivory (Scherber et al. 2006; Scherber et al. 2010), leading to the conclusion that plant species richness is not a major driver of herbivory. That might be because species richness is only a coarse and very simple descriptor for diversity within ecological communities. Other descriptors like community phylogenetics can integrate information on various plant traits, which might be related to herbivory but often are difficult to assess (for instance biochemical defense mechanisms; Wink 2003) into a phylogenetic diversity index. Several studies already focused on the effect of community phylogenetics, in addition to species richness, on herbivory and showed that increasing phylogenetic diversity of plant communities is often associated with decreasing herbivory (e.g. Castagneyrol et al. 2014; Dinnage 2013; Yguel et al. 2011) supporting the associational resistance hypothesis. Compared to this, only few studies have found a positive effect of phylogenetic diversity on herbivory (Parker, Burkepile, Lajeunesse, & Lind 2012; Schuldt et al. 2014). However, to date, most studies on phylogenetic diversity and herbivory have been carried out in forests and/or artificial or experimental communities, and thus, are lacking information about the processes in semi-natural communities under "real-world" conditions, particularly in grasslands.

Previous studies on the effects of phylogenetic diversity on herbivory have used two approaches to assess herbivory. In the first approach, herbivory is measured on one ("focal") plant species in monocultures/low diversity plots and within high diversity plots. In a recent meta-analysis, using this approach, Castagneyrol et al. (2014) showed that herbivory on trees in mixed and pure forests depended on herbivore specialization and plant phylogenetic diversity. While damage caused by specialist herbivores was related only to the abundance of their focal host plants, herbivory caused by generalists decreased in mixed forests, but only when host trees and associated trees were distantly related. In a second approach, herbivory is measured at the community level, where herbivory on all plant species is assessed. Using this measure of herbivory, Dinnage (2013) showed that although herbivory decreased weakly with increasing plant phylogenetic diversity, there was a significant interaction between plant species richness and phylogenetic diversity. Increasing plant species richness increased invertebrate herbivory, but the strength of this effect decreased with increasing plant phylogenetic diversity. By contrast, a meta-analysis by Parker et al. (2012) found an increase of herbivore damage with increasing phylodiversity of plants. The authors explained this pattern with increasing generalist herbivore damage. The contrasting results indicate that the strength and direction of the effect depend on the system studied and consequently on plant and herbivore community composition (e.g. functional composition of plant communities, specialist-generalist ratio, feeding guilds). For example, Dinnage (2013) excluded grasses from his analyses and focused only on forbs. However, grasses dominate grassland communities in terms of abundance and therefore are an important resource for herbivores. At the same time grass occurrence decreases phylogenetic diversity of plant communities especially when plant abundance is considered. Thus, in studies focusing on invertebrate herbivory in natural or semi-natural grasslands, the abundance of grasses could directly and indirectly (via decrease in plant phylogenetic diversity) affect herbivory.

In addition to biotic interactions, anthropogenic pressure (i.e. land-use intensification) can affect invertebrate herbivory. Gossner et al. (2014) showed that invertebrate herbivory in temperate managed grasslands decreased with increasing land-use intensity at the local scale. The authors hypothesized that several direct and indirect effects of increased land-use intensity might cause a decrease in herbivory, e.g. direct effects of mowing on herbivores by killing arthropods or indirect effects via reduced plant species richness and an increased proportion of grasses. At the same time land-use intensification has been shown to decrease phylogenetic diversity of plant communities (Dinnage 2009) and thus, an indirect effect of land use on herbivory might also be caused by changes in phylogenetic diversity.