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Plant traits link hypothesis about resource-use and response to herbivory

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Abstract

Grazing by large herbivores, in interplay with environmental productivity, is a key driver of the composition of the vegetation with important consequences on the ecosystem and, consequently, for land management. We tested the predictions of the resource availability – resource–acquisition theory by assessing the extent to which community averages of plant traits, known to be related to plant growth, competitive ability and response to grazing were correlated with resource gradients within local (200 km^2) geographical ranges. Second, we assessed the applicability of the same set of plant traits to make inferences on ecological effects of grazing by sheep in alpine ecosystems in Norway, using a data set consisting of 16 sites in central Norway. We estimated grazing intensity by free-ranging sheep based on GPS telemetry, soil properties, plant species composition and species traits i.e. specific leaf area (SLA), leaf dry matter content (LDMC), leaf size and plant height. Soil fertility and the interaction between soil fertility and grazing, but not grazing intensity alone, were significantly related to plant species and traits composition. Generally, average SLA showed lower correspondence with soil fertility and grazing than the other traits. Leaf size and plant height were lowest at sites with high grazing intensity and in sites with low fertility, and increased with soil fertility in little and moderately grazed sites, but declined at high fertility sites when grazing was intense. LDMC showed the opposite trend. Grazing intensity was more related to the variability in plant composition and average plant traits when environmental productivity was high. Our results therefore are indicative of a convergence of responses to grazing and nutrient limitation.

Zusammenfassung

Die Beweidung durch große Herbivore stellt im Zusammenspiel mit der Produktivität der Umwelt einen Schlüsselfaktor für die Zusammensetzung der Vegetation dar und hat damit große Auswirkungen auf das Ökosystem und dementsprechend für die Landpflege. Wir untersuchten die Vorhersagen der Ressourcenverfügbarkeits-Ressourcenerwerbs-Theorie indem wir abschätzten, in welchem Ausmaß die durchschnittlichen Pflanzeneigenschaften einer Gesellschaft, die erwiesenermaßen mit dem Pflanzenwachstum, der Konkurrenzfähigkeit und der Reaktion auf Beweidung zusammenhängen, mit den Ressourcengradienten innerhalb von lokalen geografischen Bereichen (200 km^2) korreliert sind. Wir bewerteten zweitens die Anwendbarkeit der gleichen Auswahl von Pflanzeneigenschaften für die Abschätzung von ökologischen Effekten der Schafsbeweidung auf alpine Ökosysteme in Norwegen, indem wir einen Datensatz verwendeten, der aus 16 Probeflächen in Zentralnorwegen bestand. Wir erfassten die Beweidungsintensität

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von freilaufenden Schafen mithilfe der GPS-Telemetrie, die Bodenfaktoren, die Zusammensetzung der Pflanzenarten und die Arteigenschaften, d. h. die spezifische Blattfläche (SLA), die Blatttrockenmasse (LDMC), die Blattgröße und Pflanzenhöhe. Die Bodenfruchtbarkeit und die Interaktion zwischen der Bodenfruchtbarkeit und der Beweidung, jedoch nicht die Beweidungsintensität an sich, waren mit den Pflanzenarten und der Zusammensetzung der Eigenschaften signifikant korreliert. Im Allgemeinen zeigte die durchschnittliche SLA einen geringeren Zusammenhang mit der Bodenfruchtbarkeit und der Beweidung als die anderen Eigenschaften. Die Blattfläche und die Pflanzenhöhe waren auf Flächen mit starker Beweidung und auf Flächen mit geringer Fruchtbarkeit, am geringsten, nahmen aber mit der Bodenfruchtbarkeit in gering und mittelstark beweideten Flächen zu und nahmen in fruchtbaren Flächen bei starker Beweidung ab. LDMC zeigte den gegenläufigen Trend. Die Beweidungsintensität war stärker mit der Variabilität in der Pflanzenzusammensetzung und den durchschnittlichen Pflanzeneigenschaften verbunden, wenn die Produktivität der Umwelt hoch war. Unsere Ergebnisse weisen daher auf eine Konvergenz der Reaktionen auf Beweidung und Nährstofflimitierung hin.

Keywords: Sheep grazing; Alpine plant communities; Tolerance; Resistance; Soil fertility; Alpine ecosystem; Free-ranging grazing; Norway; Plant–herbivore interactions; Sheep

Introduction

The effects of herbivores on plant communities and ecosystems may result in a community dominated by highly productive, fast-growing species or by slow-growing species, with a predominance of attributes that deter herbivory (Briske 1996; Huntly 1991). The outcome is thought to result from the interaction between the amount of resources available for plant growth and the temporal pattern of herbivory (Augustine & McNaughton 1998).

Increasing evidence supports the notion of a primary axis of specialisation in plants along resource gradients (Chapin, Autumn, & Pugnaire 1993) from acquisitive in productive habitats to retentive in chronically unproductive habitats (Grime 2006). The adaptations of plant resource-use and acquisition have a linkage to the strategies of plants to cope with herbivory. Parallel to the trade-off in resource capture strategies, two contrasting strategies to cope with herbivory have been postulated: tolerance and avoidance (Huntly 1991). Tolerance to herbivory (Briske 1996) is the capacity "*of growing more rapidly following defoliation*". It is associated with the capacity to rapidly restore lost tissues through high tissue turnover rates and rapid resource capture, thus an important strategy for plants with high growth rates (del-Val & Crawley 2005). In contrast, the avoidance strategy consists of minimising tissue loss (Huntly 1991), through several deterrent mechanisms, some of which are related to adaptations for resource acquisition and growth, since plant traits that confer ecological specialisation to resource-poor environments also result in low palatability and nutritive value for herbivores (Fine et al. 2006). In contrast, high growth rates are often associated with properties such as high levels of sugars and amino acids that are attractive to herbivores (Pérez-Harguindeguy et al. 2003).

Plant strategies to cope with herbivory are therefore linked to feed quality and hence, with herbivore selectivity and defoliation intensity. Plant responses to herbivory can trigger self-strengthening loops, in which grazing promotes forage of above-average quality (Augustine, McNaughton, & Frank 2003), but how these processes vary within scales and ranges of environmental variation and degree of herbivory is poorly understood.

Further, it has been postulated a convergence in plant attributes that confer tolerance to resource scarcity and herbivory avoidance (Grime et al. 1997). This convergence has been identified along rainfall (Milchunas & Lauenroth 1993) and fertility gradients (Grime et al. 1997), but the examination of these relationships is still incipient (de Bello, Lepš, Sebastià 2005; Fine et al. 2006) and the knowledge about the significance of spatial scales and ranges of environmental gradients limited. In the past decade, a comprehensive work on eco-physiological attributes of plants has identified a series of traits that are generally fair predictors of plant relative growth rates (Cornelissen et al. 1999), competitive ability (Grime et al. 1997), tolerance to environmental harshness (Wright & Westoby 1999), and palatability (Díaz et al. 2004). Díaz et al. (2004) extended this approach to the prediction of functional changes in plant communities by linking plant traits to ecosystem processes.

In this study, we used a data set consisting of vascular plant species composition, community averages of plant traits, soil physical and chemical properties and a quantitative assessment of forage patch use by free-ranging sheep to (i) test the resource acquisition traits – resource availability theory at the plant assemblage level and at local (ca 200 km^2) geographical ranges by assessing the extent to which a set of plant traits, generally known to be related to plant growth,