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Decomposing the land-use specific response of plant functional traits along environmental gradients

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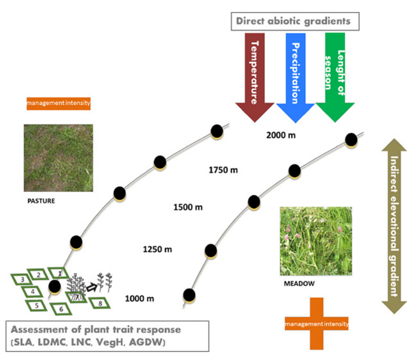
HIGHLIGHTS

- Environmental conditions affect functional trait response and thus shape ecosystems.
- We assessed the interactive effects of different environmental drivers on plant traits.
- Along 1000 m of elevation we studied how these are modulated by management.
- Management intensity attenuated response ranges of traits to climatic gradients.
- We highlight the implications of ecosystem management for plant trait based modelling.

GRAPHICAL ABSTRACT



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ABSTRACT

Environmental conditions affect functional trait variability within communities and thus shape ecosystem properties. With the ability of plants to adapt morphologically and physiologically to changing abiotic conditions, gradient analysis was shown to be a suitable tool to identify the drivers which determine trait values. Apart from direct environmental drivers and indirect gradients such as elevation, also anthropogenic effects (e.g. irrigation, grazing) can influence trait variability. Our aim was to assess the interactive effects of different environmental drivers on major plant traits and to investigate how these are modulated within two different land-use types (hay meadow vs. pasture). An elevational gradient spanning 1000 m was decomposed into its underlying direct components (temperature, water input, length of growing season) for the investigation of gradual responses of five prominent functional traits (aboveground dry weight (AGDW), vegetative height (VegHt), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC)) for key species from two functional groups (grasses, forbs) in the two land-use/management regimes. The present study revealed that the detailed analysis of single direct gradients provides substantial additional information on trait response which remains hidden or is even reversed if only indirect gradients such as elevation are analysed. However, trait response to the combination of the three direct gradients aligned surprisingly well with trait response to the indirect gradient underpinning the adequate representation of temperature, water input and length of growing season by elevation. The response of traits significantly depended on the management regime and corresponding intensity which was shown to play an overriding role and constrained and attenuated response ranges of traits to climatic gradients.

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1. Introduction

The structure and function of plant communities are shaped by environmental conditions which determine the presence and relative abundance of species within a community. In addition, abiotic and biotic parameters affect the distribution and frequency of specific phenotypes and optimise the value of plastic traits within a given species of the ecosystem (Violle et al., 2012).

The ability of plants to respond dynamically to changing environmental conditions by adapting their phenotype provides a reliable tool for the assessment of the environment affecting these communities. Based on inter- and intraspecific trait value frequencies and diversity, ecosystem research has developed several approaches which seek to implement functional traits for the evaluation of ecosystem processes, functioning and health (e.g. Petchey and Gaston, 2006; Villéger et al., 2008; Pla et al., 2012). Within the scope of modelling ecosystem functions and services, approaches based on functional plant traits are being increasingly established (Lavorel et al., 2011; Fontana et al., 2014; Reichstein et al., 2014). To this end, more and more studies retrieve trait values from transregional trait databases (Kattge et al., 2011). This common and fast procedure replaces trait measurements on site, but may potentially cause inaccuracies by neglecting intraspecific trait dynamics and small scale variability (Albert et al., 2010a; Lepš et al., 2011). Several recent studies emphasise the importance of revealing the drivers of trait response within the context of functional diversity and community structure approaches (de Bello et al., 2011; Lepš et al., 2011; Violle et al., 2012).

Gradient analysis is well-suited for providing improved knowledge on how the responses of plant traits to environmental conditions affect the functioning of a community (Kichenin et al., 2013; Luo et al., 2016). Garnier et al. (2016) describe four types of environmental gradients which are responsible for variations in trait values: i) direct (e.g. air temperature, precipitation), ii) indirect (e.g. altitude), iii) resource (e.g. nutrient availability), and iv) disturbance gradients (e.g. grazing intensity). However, particular ecological gradients will usually resolve into multiple co-varying factors. An indirect gradient (e.g. changing altitude) induces variation in the direct gradients of solar radiation, air temperature, and length of growing season (Körner, 2003). Indirect gradients were reported to hide ecological patterns since they do not affect plant physiology and functioning directly (Körner, 2007; Albert et al., 2010a). Therefore, in order to understand the interaction of environmental gradients and the functional composition of ecosystems, a comprehensive analysis of the gradients involved and their impact on functional differentiation is needed.

Ecological gradients have the advantage that disturbance resulting from human activity can be disclosed (Fukami and Wardle, 2005). Anthropogenic disturbance plays an important but often neglected role in studies investigating environmental gradients. Pakeman et al. (2009) found that in managed grasslands 50% of vegetative trait variation was explained by biotic and abiotic factors, but human management was still responsible for 13% of its variation. In particular traits such as plant height, leaf dry matter content (LDMC), and specific leaf area (SLA) have been shown to respond to human management practices as for example altered grazing intensity (Díaz et al., 2001; Garnier et al., 2007; Quétier et al., 2007). The question whether human management counteracts or amplifies the effects of abiotic or biotic parameters on plant traits is still to be answered. As a consequence, the outcome of projected future changes in environmental conditions might vary with respect to management intensity at a particular site. External inputs, e.g. fertilisation or mowing, might act as a filter by sorting species with respective trait values (i.e. nitrophilous species, or species resistant to disturbance) while at the same time diminishing the intensity of natural gradients and consequently the trait response at the site.

Recent studies have found high variability of traits within species along two gradients (temperature, radiation) in an alpine valley, indicating that their response to abiotic parameters is idiosyncratic and may depend on environmental conditions (Albert et al., 2010b). In order to go beyond independent reactions of specific species, while investigating environmental effects on processes on a community level, the clustering of species into functional groups (FGs) was shown to be helpful (Symstad, 2000; Voigt et al., 2007). Species belonging to the same FG will often respond similarly, since members of a particular FG share fundamental and basic phenological and morphological characteristics (Voigt et al., 2007), while the response of different groups to the same driver might diverge (Domingues et al., 2007; Way and Oren, 2010).

Only a few studies have investigated the interactive effects of different environmental drivers on the response of plant traits along ecological gradients while tracing a steady set of plant species over the whole gradient (e.g. Pescador et al., 2015). For the present study we decomposed an elevational gradient into its direct (abiotic) components: temperature, water input, length of growing interval. For five prominent functional traits the average response to these direct and indirect environmental drivers was assessed in two land-use types with contrasting management intensity in a mountain region with low background precipitation. Trait response on lightly grazed pastures was compared with irrigated and fertilised hay meadows for grasses and forbs along an elevational gradient spanning 1000 m elevation. While the climatic conditions of the pastures followed those of the elevational gradient (i.e. decrease in temperature and increase in precipitation with increasing elevation), the meadows were irrigated, which reversed the natural gradient of water input (Fig. 1). We hypothesise that management intensity is a decisive determinant of plant trait response, overriding background climatic gradients, and specify cases where direct gradients are better suited to disclose a detailed plant trait response than indirect gradients.

2. Material and methods

2.1. Study site description

Plant sampling was conducted at the Long-Term Socio-Ecological Research (LTSER) site Matsch|Mazia valley in the province of Bolzano, South Tyrol, Italy (46.6928°, 10.6157°). The Matsch valley is characterised by strongly pronounced inner-alpine continental climate conditions (Rechenmacher, 1986; Della Chiesa et al., 2014). The average precipitation in the valley is at around 525 mm per year, the average temperature is 5.6 °C (1925–2005, at 1580 m a.s.l., Hydrographic Office of the Province Bolzano, South Tyrol). Lower elevated meadow sites (until 1500 m a.s.l.) are additionally irrigated since the natural precipitation is not sufficient for intensive hay production.

Plants were sampled within five equally spaced sections along a SW exposed altitudinal gradient spanning 1000 m. The lowest sampling sites are located at ~1000 m a.s.l. in the foothill zone and the highest ones accordingly at ~2000 m in the subalpine zone (with three intermediate points every 250 m). At each altitude, an intensively managed hay meadow (M) and a lightly grazed pasture (P) were investigated. The meadows are usually fertilised with approx. 3 kg manure per year and m^2 (corresponding to ~15 g N_{tot} per m^2), mown twice a year and artificially irrigated (see Table 1, Fig. 1). The lower meadows can be assigned to the phytosociological association of *Pastinaco-Arrhenateretum* (Passarge, 1964) at 1000 m and 1250 m a.s.l. and convert into *Trisetetum flavescentis* (Rübel, 1911) at ~1500 m a.s.l. Pastures are lightly grazed by cattle (0.5–1.5 units of livestock per ha for approx. four months a year) without additional fertilisation or irrigation. They belong to the association *Festucetum valesiacae* (Strimmer, 1974) and convert into *Sieversio-Nardetum strictae* (Lüdi, 1948) at the higher elevations (from ~1750 m a.s.l. upward). Over the last 15 years the management intensity on both land-use types was stable with regard to fertilisation, water input, mowing frequency, and grazing. Lower elevated sites had a higher content of sand (~60–65%) than sites at higher elevation (~40–