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Plant-herbivore interactions along elevational gradient: Comparison of field and common garden data

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ABSTRACT

In response to climate change, various organisms tend to migrate to higher elevations and latitudes. Unequal migration rates of plants and animals are expected to result in changes in the type and intensity of their interactions such as plant-herbivore interactions. In the present study, we studied the extent of herbivore damage in *Salvia nubicola* along an elevational gradient in Manang, central Nepal. A common garden experiment was also carried out by sowing seeds collected from different populations along the elevational gradient. As expected, the extent of herbivore damage in the field was significantly lower at higher elevations, and it increased with the population size and at sites without shrubs. In the common garden experiment, herbivore damage was higher in plants originating from lower elevations and from more open habitats. While higher herbivore pressure in the field at lower elevations may suggest that plants will be better protected against herbivores at lower elevations, the common garden study demonstrated the opposite. A possible explanation could be that plants from higher elevations have to adapt to extreme conditions, and lower palatability is a side effect of these adaptations. Thus, *S. nubicola* in the Himalayan region is likely to survive the expected higher herbivore pressure caused by an upward shift of herbivores under future climate change. Future studies should attempt to elucidate generality of such a conclusion by studying multiple species along similar gradients. Our results from comparison of the field and common garden study suggest that future experiments need to include comparisons in common environments to understand the expected response of plants to changes in herbivore pressure.

1. Introduction

Climate change is expected to have a range of effects on ecosystems all over the world (Bhutiyani, 2015; Parmesan, 2006; VijayaVenkataRaman et al., 2012). The effects of climate change on survival of various organisms are expected to be intense especially at high elevations and latitudes (Diaz and Eischeid, 2007; Parmesan, 2006; Theurillat and Guisan, 2001) because the global temperature increase will be between 1.4 and 5.8 °C by 2100 in these areas (Pachauri et al., 2014). The most direct way for organisms to respond to climate change is through migration to higher elevations and latitudes, as this enables the species to follow climatic conditions to which they were previously adapted (Bale et al., 2002; Chen et al., 2011; Nicotra et al., 2010). It has been suggested that the migration rates of plants and animals will not synchronize because plants are sessile organisms and shift much more slowly in comparison to mobile animals (Colwell et al., 2008). The unequal migration rates of plants and animals as a consequence of climate change will result in changes in the type and intensity of their interactions (Colwell et al., 2008; Cornelissen, 2011; Hillyer and Silman, 2010; Parolo and Rossi, 2008). The interactions between plants and their herbivores are likely to have the strongest effects on the performance of plant populations (Agrawal et al., 2012; Crawley, 1989). Understanding the intensity of plant-herbivore interactions and their variation under different climatic conditions is thus an important prerequisite for predicting species response to future climate change (Van der Putten et al., 2010).

Elevational gradients are perfect systems to study the intensity of plant-herbivore interactions in relation to climate because of the steep changes in temperature and precipitation along these gradients (Körner, 2007). In general, the intensity of herbivore damage decreases with increasing elevation (Andrew et al., 2012;

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Hodkinson, 2005). This could be caused by various factors such as temperature, moisture, type of vegetation and soil composition (Klapwijk et al., 2013; Rodríguez-Castañeda, 2013; Schuldt et al., 2012). It has been found that reduced herbivore diversity and abundance at higher elevations is strongly linked to changes in a range of plant traits along the elevational gradient, such as reduced plant size (Schlinkert et al., 2015), lower physical resistance (Carmona et al., 2011) and lower content of anti-herbivore defences in plants from higher elevations (Pellissier et al., 2014; Rasmann et al., 2014; Zidorn, 2009).

Most of the studies looking at plant-herbivore interactions along elevational gradients have done so in the field exploring plant performance in natural populations (e.g., Alonso, 1999; Pellissier et al., 2012). However, the differences in plant traits and plant-herbivore association along elevational gradients observed in field studies may be caused by genetic differentiation of the plant populations or may just reflect a plastic response to the local environment or differential abundances of the herbivores (Cordell et al., 1998; Jonas and Geber, 1999; Ohsawa and Ide, 2008). While the former would suggest that upward herbivore migration may represent an important threat to the plant populations, the latter would suggest that the plants are in fact quite well able to cope with climate change and modify their performance according to the environment. Separating these two possibilities is thus necessary to understand the possible consequences of future climate change. For this, several previous studies exploring physiological and morphological traits and reproductive phenology have used common garden experiments to compare plants originating from different locations along elevational gradients (Cordell et al., 1998; Gugger et al., 2015; Jonas and Geber, 1999; Preite et al., 2015; Rudgers and Whitney, 2006). In contrast to the studies exploring the effects of the elevation of origin on plant traits using common garden experiments, only a single study (Rudgers and Whitney, 2006) has used a common garden experiment to compare the susceptibility of plants from different elevations to herbivores and compared the patterns between the field and the common garden. The comparison of field-based data and common garden experiments allows us to see how herbivore damage to individuals from different populations varies along an elevational gradient. By exploring the mechanisms of this difference in the common garden, it is possible to predict the consequences of upward herbivore shifts due to warming in the future.

In this study, we investigated the patterns of herbivore damage in *Salvia nubicola* in Nepal, in the central Himalayan region, and explored the factors influencing herbivore damage. *Salvia* species are widely distributed and contain many phenolic compounds that are important for plant defence against herbivores (Daayf et al., 2012) because they can act as anti-feeding agents, antioxidants or signalling molecules (Boeckler et al., 2011; Shalaby and Horwitz, 2014). Most species of *Salvia*, including *S. nubicola* also produce different volatile organic compounds, specifically essential oils stored in their glandular trichomes (Dostálek et al., 2016; Kesselmeier and Staudt, 1999; Melkani et al., 2011), that are herbivore repellent. *S. nubicola* has a wide distributional range from 2100 to 3600 m asl and is easy to cultivate (Dostálek et al., 2016; Press et al., 2000). Moreover, it is damaged by herbivores at different intensities of herbivory at different elevations (Dostálek et al., 2016). All of these factors make *S. nubicola* a perfect model species for assessing patterns of herbivore damage along a wide elevational gradient. To determine if the observed patterns of herbivore damage in *S. nubicola* are due to different levels of herbivore pressure or different conditions at different elevations or if the differences are linked to genetic differences in the plants, we studied the plant-herbivore interactions both in the field and in the common garden, growing plants from different elevations in a single location. To do this, we used 27 populations of *S. nubicola* growing along an elevational gradient from 2050 to 3493 m asl in Manang district, central Nepal, representing an approximately 7 °C difference in the mean annual temperature. We predicted that herbivore damage will decrease with increasing elevation (decreasing herbivore pressure) and that plants from lower elevations will thus be more adapted to herbivore damage and thus more resistant to herbivory. Another possibility might be that plants could respond to increased herbivore pressure not by increased resistance but by increased tolerance when plants can regrow after herbivore damage (Schoonhoven et al., 2005). However, in our previous study (Dostálek et al., 2016), we showed that there were no differences in compensatory growth after herbivore damage in *S. nubicola* plants from different elevations. This is why we only focus further on plant resistance rather than tolerance.

2. Methods

2.1. Study species

Salvia nubicola Wall. ex Sweet (Lamiaceae) is a common perennial herb with a quadrangular stem that grows up to 60–150 cm. The leaves are stalked, dentate and hairy with a hastate base. The flowers are yellow and occur in large, spreading panicles. This species flowers and produces fruits from June to October. The seeds fall onto the ground after maturation and germinate when the environment begins to warm in April–May. Although the exact mechanisms of seed dispersal are not yet known, the seeds are thought to be dispersed by wind, water or animals, as in other species of *Salvia* (Huisinga, 2001). This species is distributed in western and central Nepal from 1800 to 3600 m asl in open areas with humus-rich soils. It also occurs in Afghanistan, Bhutan, northern India, Pakistan and Tibet (Press et al., 2000). In Nepal, the decoction of roots is used against fever (Manandhar, 2002). It is mostly eaten by caterpillars of several insect such as lepidopteran larvae and different kinds of beetles and their larvae (Rokaya et al., unpublished data).

2.2. Study populations and herbivore damage in the field

We randomly selected 20 different mature flowering individuals at each population. In total, there were 27 populations along an elevational gradient from 2050 to 3580 m asl in Manang district, central Nepal (Appendix A). For each plant individual, the herbivore damage of five different leaves along the stem was recorded in percentages. In addition to the leaf damage, the height of the longest stem of each plant (hereafter referred to as *plant height*) was recorded. To cover the temporal variability in herbivore damage, the data were collected at the three different times for each population: the first during the third and fourth week of August 2013, the second during the second week of July 2014 and the third during the third and fourth week of August 2014.

At the population level, we estimated the total number of all flowering *S. nubicola* individuals (hereafter referred to as the *population size*), the habitat openness (0-open sites with no or very little tree shading; 0.5-open sites with scattered shrub or tree shading; 1-sites in the forest), and the presence or absence of shrubs in the vicinity of each population.

2.3. Common garden experiment with herbivore damage

We collected seeds from seven randomly selected mother plants in each of 25 populations from 2050 to 3260 m asl during seed maturation in October 2013 (Appendix 1). In March 2014, seven seeds from each mother plant were sown in a pot in the common