Plant consumer effects on plant allometry

Testing the hypothesis that the allometry of plant height explains that invertebrate herbivory and pathogens increase light availability to increase plant diversity

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Aims and Background

Invertebrate herbivores and pathogenic fungi might reduce community biomass, and thereby enhance light availability and promote plant diversity (Cappelli *et al*. 2020; Descombes *et al*. 2020; Zhang *et al*. 2024). Although light competition has been verified as a main cause of species loss under large herbivore exclusion and nutrient enrichment (Borer *et al*. 2014; Xiao *et al*. 2021; Eskelinen *et al*. 2022), direct evidence for the light competition in regulating diversity under invertebrate herbivory and pathogen exclusion has been scarce. The intensification of light competition may lead to plants growing taller and thinner. The allometry of plant height provides a feasible way to indicate a species "shape" strategy in acquiring light resources (Xiao *et al*. 2021). Allometric scaling laws (West *et al.* 1999; Brown *et al.* 2004) predict that plant heights of vascular plants can be expressed as the allometric function: $\mathrm{Y} = Y_0 M^b$ or $\log_{10}\mathrm{Y} = \log_{10}Y_0 + b\log_{10}M$, where Y is plant height, M is plant size (such as individual biomass), Y_0 is the plant height when M = 1, b is the scaling exponent, and $\log_{10}Y_0$ is the intercept (Fig. 1). The negative height allometric scaling (Fig. 1a, $b < 1$) indicates that the height growth rate decreases as size increases, allowing smaller plants (i.e., before the threshold of 1-unit height) to grow taller and thinner (size-specific) in short temporal windows and provides a size-specific advantage to reach light resources (Enquist *et al*. 2007). The intercept ($\log_{10}Y_0$) reflects the baseline level of plant height and is supposed to infer the plant height of relatively large individuals in a grassland system where the sizes of most plant individuals are smaller than 1 unit (e.g., 1 g). So, a lower height scaling exponent and a higher intercept can provide species with the advantage of population-level height growth, thereby enhancing their competitiveness for light resources. Thus, we intend to calculate the allometric size-height relationships of the dominant species growing in a site to test whether light competition might potentially drive species loss under invertebrate herbivory and pathogen exclusion.

We aim to test the following hypotheses: *i*) Invertebrate herbivory and pathogen exclusion decrease light penetration, favoring species grow thinner and taller with lower species-specific height scaling exponents and larger intercepts (Fig. 2a); *ii*) abundant species develop a stronger competitive capability for light resources with lower height scaling exponents and higher intercepts, comparing to rare species, under invertebrate herbivory and pathogen exclusion (Fig. 2b); *iii*) invertebrate herbivory and pathogen exclusion reduce species diversity through reducing light penetration and excluding species that lack shape advantages in light competition (i.e., with higher scaling exponents and lower intercepts); *iv*) light competition plays a stronger role in driving species loss caused by invertebrate herbivory and pathogen exclusion in wet and fertile environments; *v*) the interaction between enemies can amplify or diminish the effects of each individual enemy on the allometry of plant height and plant diversity.

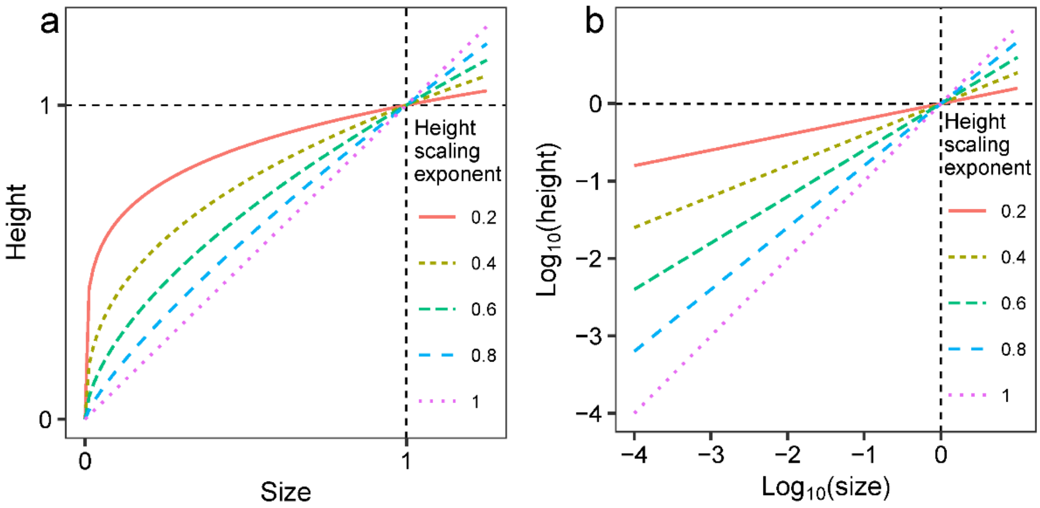

Figure 1. Illustrations of the allometric height growth with size (individual mass) showing in origin data (**a**) and $\log_{10}$-transformed data (**b**). Lines in different colours represent different values of the height scaling exponent *b*.

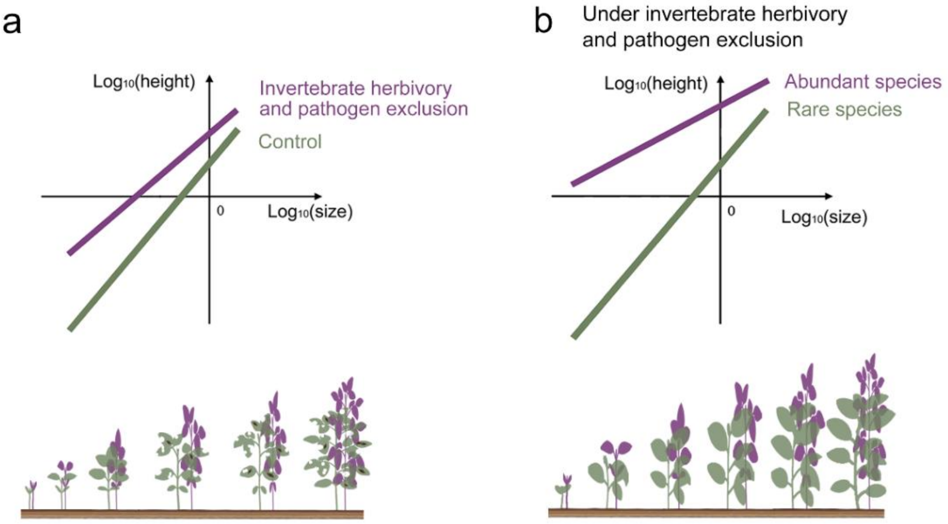

Figure 2. Hypothesized change of the allometry of plant height under invertebrate herbivory and pathogen exclusion. **a**, Invertebrate herbivory and pathogen exclusion might decrease light penetration, favoring species grow thinner and taller with lower species-specific height scaling exponents and larger intercepts. **b**, Compared to rare species, abundant species might grow thinner and taller without the suppression of invertebrate herbivores and pathogenic fungi, thus possessing a stronger ability to acquire light resources.

Detailed protocol

We will include only the following treatments: control, insects (I), molluscs (M) , fungi (F) and all three (I, M, F) exclusion treatments, with three replicates each this gives 15 plots in total. On these we will take the following measurements at the peak of growing season:

1) Light penetration

At the peak of growing season, we measure the ***photosynthetic active radiation*** (PAR) at the ground and above the plant community of each plot, with three replicates on cloudless days at noon, using a Sunfleck PAR Ceptometer (AccuPAR LP-80, METER Group, Inc. USA). For each replicate day, PAR measurements are taken at three randomly selected locations within each plot. The use of other PAR sensors is also possible.

2) Plant height and dry biomass

We then select the 7 most common plant species (including both grasses and herbs) in terms of cover in the control plots. One these plant species we will do our allometry measurements. We randomly select up to 7 individuals for each of the seven plant species in each plot of the above mentioned treatments (control, I, M, F, IMF). The whole plot area can be used to find the individuals, except of the core plot. It might be difficult to find 7 individuals of every species in every plot. In this case you can collect more individuals in other plots of the same treatment to always have a minimum of 15 individuals per species and treatment. This would result in a total of max. $7 \times 7 \times 15$ plots = 735 individuals, and min. $7 \times 15 \times 5$ treatments = 525 individuals.

We visually define individuals for grasses as plants forming a small clump or tussock (or ramet), having significant gaps with neighbors at the base, or having independent roots or stems. On each individual, we measure the ***maximum height*** (height after being stretched, measured to 0.1 cm) and ***natural height*** (natural height without stretching, measured to 0.1 cm, including reproductive structures) in the field. We then cut the aboveground part of each individual above the ground and store it in a labelled paper bag. The ***aboveground mass*** (g) of each individual should be weighed to 0.001 g after drying 3 days at 65℃.

3) Species cover or species biomass

We use species cover to calculate species relative abundance and species diversity of each plot. These data are taken from the core plot (as part of the normal BugNet sampling).

4) Soil fertility

We use the soil properties (such as total carbon, total nitrogen, available phosphorus and water content) under natural conditions or under control to represent the soil fertility of each site, which have been taken already within the baseline measurements.

Outline of the analysis

1) Quantifying the height scaling exponent and intercept

We will calculate the species-specific height scaling exponent and intercept of each target species under each treatment based on the allometric equation (West *et al*. 1999), using standard major axis regression with sma function in smatr package (Warton *et al*. 2012):

$$\log_{10}\mathrm{Y} = \log_{10}Y_0 + b\log_{10}M$$

where *b* is the height scaling exponent (the slope of the linear function), $\log_{10}Y_0$ is the intercept of the linear function, Y is plant height (cm), *M* (g) is the plant size (individual dry biomass) and Y_0 equals to the plant height when plant size = 1 (g, $\log_{10}1 = 0$).

2) Quantifying the light penetration

We use the light penetration to represent the light availability.

3) Analyzing the species-specific height scaling exponent and intercept
4) Analyzing light penetration and the community-level allometry of plant height
5) Analyzing the relationship between the relative abundance and the species-specific height scaling exponent/intercept
6) Analyzing the relationship between the species relative abundance and the response of the species-specific height scaling exponent/intercept
7) Analyzing the relationship between the response of the species relative abundance and the response of the species-specific height scaling exponent/intercept
8) Analyzing the response of species richness
9) Assessing the causal relationships between treatments and species richness

References (optional)

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