Plant Biosystems (2026) 160:93
https://doi.org/10.1007/s44473-026-00111-x

RESEARCH

The hummocky meadow micro-scale patchiness effect on the Eggleaf twayblade *Neottia ovata* (Orchidaceae) functional traits

Igor Paušič[1] · Tomaž Granda[2] · Klavdija Pliberšek[1] · Peter Kozel[1,3]

Received: 27 January 2026 / Revised: 28 January 2026 / Accepted: 7 February 2026 /
Published online: 20 February 2026
© The Author(s) 2026

Abstract

Regularly managed hummocky meadows represent a species-rich, distinct type of post-glacial grassland communities, which appear on loose carbonate material. Such micro-reliefs are characterized by numerous humps and pits, i.e. convex and concave features of the surface. Little is known about how plants respond to environmental heterogeneity at such small spatial scales. *Neottia ovata* (Orchidaceae) is a member of the Eurosiberian, Boreo-temperate element. This species is a well documented habitat generalist, occupying a wide range of habitats ranging from lowlands to mountains and from wet to dry sites, often including anthropogenic habitats. The aim of the present study was to evaluate the effect of hummocky meadow micro-scale habitat patchiness, i.e. small-scale habitat heterogeneity on selected *N. ovata* functional traits. Across all generalized linear mixed models (GLMMs), plant micro-location on the slope of a hump, expressed as plant height on a hump index was the key predictor of the analysed functional traits. The specific micro-location of *N. ovata* specimens on the meadow humps plays a vital role in the plant's functional trait values; it also affects fitness and the percentage of pollinated flowers. Hummocky meadow micro-scale patchiness offers interesting perspectives for further research. Protecting the remaining hummocky meadows contributes to the conservation of biodiversity of the fragile alpine environment.

Keywords *Neottia ovata* · Orchids · Hummocky meadows · Habitat micro-scale patchiness · Functional trait variability · Environmental parameters

✉ Igor Paušič
igor.pausic@um.si

[1] Biology Department, Faculty of Natural Sciences and Mathematics, University of Maribor, Koroška C. 160, 2000 Maribor, Slovenia

[2] Biotechnical Faculty, University of Ljubljana, Jamnikarjeva 101, 1000 Ljubljana, Slovenia

[3] Karst Research Institute, Research Centre of the Slovenian Academy of Sciences and Arts, Titov Trg 2, 6230 Postojna, Slovenia

Introduction

The environmental heterogeneity hypothesis holds that spatial heterogeneity in biotic and abiotic environmental conditions increases biodiversity (Macarthur and Wilson 1967; Ricklefs 1977). This relationship seems to be highly scale- and potentially resource dependent, lending support to the assumption that soil chemistry, texture, and depth, for example, have the greatest impact on community composition at small spatial scales, with climatic variables becoming increasingly important as scale increases (Costanza et al. 2011). At micro scales, environmental heterogeneity within communities is assumed to support resource partitioning between competing species (Bolker 2003; Costanza et al. 2011). In contrast, at the local-patch scale; small-scale soil or resource heterogeneities can provide dissimilar niches, possibly favouring particular individuals of competing species (Olagoke et al. 2023) or providing optimum conditions for a single species. Little is known about how the plants respond to environmental heterogeneity (hump-pit topography) at such small spatial scales (Bell and Lechowicz 1994; Kephart and Paladino 1997).

The treethrow hump-pit microtopography, i.e. hummocky meadows, represents a specific type of grassland surface, that occurs on loose carbonate material. This type of meadows has been studied mainly by German-speaking researchers (Penck 1940/41) and named 'Buckelwiese' (German: Buckelwiese, literally 'hummocky meadow') with evidence from the Alpine areas including Slovenia. Erosion itself plays a key role, however it still remains unclear which process triggers the initial formation of such micro-geomorphological surfaces. The hillslope topography (hummocky meadow) was also interpreted as an effect of simultaneous congelifluction (Dylikowa 1956), meaning a relatively slow and long-term soil flow over permafrost or within a periglacial zone. Later on, a new model of the formation of this topography was introduced, proposing that the hump-pit micro-topography was due to the uprooting of trees caused by a strong wind events (Gerlach 1960).

The species composition and distribution of alpine meadow plants are influenced by a variety of factors lasting over a long period, including climate, soil, water, topography, and plant biological characteristics (Zhang et al. 2021). Among abiotic factors, topographical factors have a strong impact on plant growth (Davies et al. 2007), especially when the research scale is small. Topography at the local scale is one the most important factors affecting vegetation; species composition (Swenson et al. 2010), plant growth (Hara et al. 1996; Sakai and Ohsawa 1994), and the spatial distribution of plant populations (Palmer and Dixon 1990).

According to Prezelj (2012) and regarding hummocky meadow micro-topography; shallower soil, faster drying, and lower amount of the remaining moisture is characteristic at the top of the humps compared to pits. The soil of the larger humps dries faster in comparison to medium and small humps. The position on the hump, size of the hump and insolation affect the vegetation composition and species richness (Prezelj 2012). At the top of the humps the vegetation typical for drier and shallower soils is found. Pits are characterized by the vegetation of moist, deeper and fertile soil. Species diversity is greatest in the middle of humps (Prezelj 2012). Differences in functional group composition were also observed: moss cover increased towards the top of the hump, and the grass cover, inversely, decreased. The proportion of clay on the hump is smaller than in the depression (pit), which indicates that the particles are washed into the depression.

Neottia ovata (L.) Bluff & Fingerh. is a sturdy, robust species: it can thrive without mycorrhiza, the rhizome of adult plants is free of mycorrhizal colonization (Kotilínek et al. 2015), and it flowers continuously for over 20 years, pollinated by the numerous insects

(Coleoptera, Hymenoptera and Diptera) attracted to the abundant nectar (Delforge 2006). *N. ovata* is self-compatible but has a well-developed rostellum to prevent self-fertilization (Talalaj et al. 2017). It is a rewarding species, with a Eurasian distribution and has also been reported as introduced in Ontario (Canada)- very widespread and common in the temperate zone but rare in the Mediterranean regions of Europe. Preston and Hill (1997) include *N. ovata* as a member of the Eurosiberian, Boreo-temperate element. A habitat generalist, it occupies a wide range of habitats from lowlands to mountains and from wet to dry sites, including anthropogenic sites (Kotilínek et al. 2015). It is a perennial herb whose populations are maintained predominantly by sexual reproduction, as vegetative spread is limited. *N. ovata* is a long-lived species, as shown in the long-term observations of Tamm (1991). Due to its longevity, the species is a suitable indicator of recent land-use changes. Variation of flower structure and nectar chemistry and their weak correlation with reproductive success confirms the generalistic character of *N. ovata* (Brzosko et al. 2021) regarding effective pollinators.

The aim of the present study was to evaluate the effect of hummocky meadow micro-scale habitat patchiness, i.e. small-scale habitat heterogeneity on selected *N. ovata* functional traits. The following two questions were addressed: (i) how does specific hump location ecologically affect measured functional trait values and (ii) is there an ecological optimum hump location for *N. ovata* considering the observed functional trait values?

Materials and methods

Study area

In order to minimize the impact of certain, site-specific environmental factors such as altitude, meadow exposure, shading effects, slope of the terrain, meadow management regime, etc. a single hummocky meadow was sampled in this study. The studied meadow is located in the NE part of Triglav National Park, NW Slovenia (Fig. 1), at an average altitude of 1350 m and covers an area of 0.65 ha. This meadow is enclosed on all sides by forest except on its SW side, where it borders a paved road leading towards the Vršič pass (1611 m, centroid point: 46°26′22.84"N, 13°45′22.43"E). Based on the site conditions, the potential forest vegetation of this stand, dominated by *Picea abies*, *Fagus sylvatica* and *Larix decidua*, belongs to the association *Polysticho lonchitis-Fagetum* var. geogr. *Anemone trifolia*.

In-situ data collecting

On site we examined 382 flowering *N. ovata* specimens from 23 humps. Following functional character values; plant height and inflorescence length were obtained *in-situ* using a digital beak scale, number of flowers and number of fertilized flowers were counted in the field for each specimen. Total leaf area for each specimen was obtained using a digital camera and ImageJ, open-source software package for processing and analysing scientific images. For leaf chlorophyll content a non-destructive measurement was performed using SPAD-502 Plus device. The SPAD value, determined by SPAD-502 provides an indication of the relative amount of chlorophyll present in plant leaves, which can serve as an indicator of the overall condition of the plant itself. Two measurements (for both leaves) per plant were taken, the average values were used for further analysis. Vegetation height

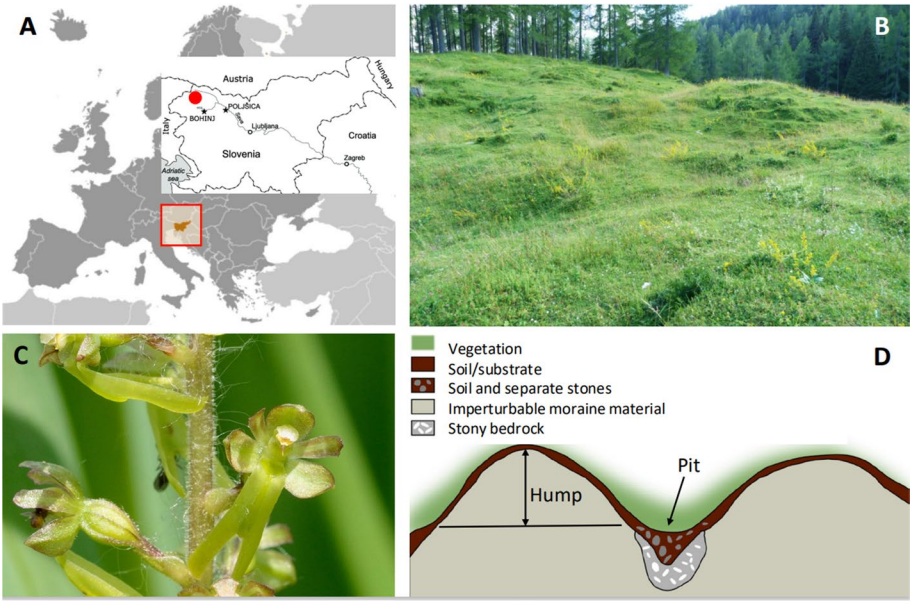


Fig. 1 Geographic location of the sampled hummocky meadow (**A**), sampled hummocky meadow (**B**), *N. ovata* flower close up and (**C**) hump cross profile (**D**)

of the surrounding grass (turf) cover at close vicinity of each plant was measured together with substrate depth. For each plant the hump location was observed and measured; vertical distance from the hump base and the plant location. Since humps vary in their height, plant height on a hump index for each plant was calculated: plant height on a hump/total hump height. Value 0 indicates location at the base of the hump while the value 1 means the summit location. Hump slope inclination was calculated: hump total height and horizontal distance: hump summit-hump rim, were measured in the field. For each hump, slope inclination was calculated later on using angular functions.

Data analysis

First, to describe the data structure, we calculated means with standard deviations (SD), medians with interquartile ranges (IQR), and the coefficient of variation for all variables. The Kolmogorov–Smirnov test was used to check whether values of variables departed significantly from normality. Redundancy analysis (RDA) was initially conducted to explore the relationships between plant functional traits and environmental variables (micro-relief, substrate depth and turf height) and to evaluate the relative influence of environmental variables on plant functional traits. To account for differences in scale, environmental variables were standardized prior to analysis. To assess multicollinearity among environmental variables, we calculated the Variance Inflation Factor (VIF). Variables with a VIF greater than 3 were removed to reduce multicollinearity and ensure the stability of the RDA results. The statistical significance of the model, axis and environmental variables was evaluated using the Monte Carlo permutation test with 999 permutations. The ordination analysis was conducted in vegan R package (Oksanen et al. 2025). To explore the effect of micro-relief, also

substrate depth and vegetation (turf) height, on the variability of the functional traits of *N. ovata*, we applied generalized linear mixed models (GLMMs). Through the mixed procedure, we addressed spatial dependency arising from repeated measurements of plant traits on the same hump by specifying the hump as a random factor. Plant height, inflorescence length, number of flowers, number of fertilized flowers, percentage of fertilized flowers, leaf area, and leaf chlorophyll concentration were used as dependent (response) variables. All the measured plants were classified into quartiles based on their functional trait values. Since we were interested in the effect of micro-relief, we present in discussion the first quartile (Q1, N = 95), which comprised the highest values of the measured functional traits more in detail. Values of dependent variables were modelled using a negative binomial distribution family, a distribution applied for over-dispersed count data (Zuur et al. 2009; Zuur and Ieno 2016). The following independent (explanatory) variables were addressed as potential predictors of the dependent variables: hump height (Hump_H), plant height on a hump (PlantH_Hump), plant height on a hump index (PlantH_HumpInd), hump slope inclination (Hump_Inc), substrate depth (Sub_D) and vegetation height (Veg_H). Prior to model fitting, to avoid common statistical problems, a detailed exploratory data analysis was conducted in accordance with the standard procedures for regression-type analyses (Zuur et al. 2010; Zuur and Ieno 2016). Accordingly, the presence of outliers in response and explanatory variables was visually checked with Cleveland dot plots. Multi-collinearity among variables was assessed using Pearson correlation coefficients and variance inflation factors (VIF), with cutoff values of $r \geq \pm 0.7$ and $VIF > 3$ (Zuur et al. 2013). Possible non-linear effects of continuous variables in the models were examined using generalized additive models (GAM) with the gam R package (Hastie 2023). Similarly to the RDA analysis, the variables were standardized prior to model fitting to account for differences in their scales. After fitting the initial models, including all noncollinear variables of interest, we conducted model selection. A backward elimination procedure was chosen, whereby variables were progressively deleted according to corrected Akaike information criterion (AICc), with lower values indicating better models (Burnham and Anderson 2002). Since in some cases we found high model uncertainty, i.e. similarly high AICc weights in two or more models, we applied model averaging for models with similar AICc weights, since this procedure provides a robust means of obtaining parameter estimates (Burnham and Anderson 2002). Both model selection and model averaging were carried out in the MuMIn R package (Bartoń 2025). Given the nearly equal Akaike weights of the two models predicting leaf area, model averaging was performed using conditional averaging, which estimates effects only from models that include each variable. This approach highlights the contributions of variables supported by the model set. Model validation was carried out on the final models (Zuur et al. 2009, 2013; Zuur and Ieno 2016). All GLMMs were fitted with the glmmTMB R package (Brooks et al. 2024). Surface plots were created in the rgl R package (Murdoch and Adler 2023). All statistical analyses were carried out in the R version 4.1.2 (R Development Core Team 2021).

Results

Descriptive statistics for all variables included in the analysis are shown in Table 1. Data exploration revealed the presence of two outlying values in the independent variable vegetation (turf) height, so they were removed from the dataset. The independent variable hump height was not included in the initial models because it was collinear ($r > 0.7$; $VIF > 3$) with

Table 1 Descriptive statistics for the independent variables (micro-relief, pedological and vegetational characteristics) and the dependent functional traits of *N. ovata*. Variables with non-normally distributed data are in bold

Independent variables	Hump height (cm)	Plant height on a hump (cm)	Plant height on a hump index	Hump slope inclination (°)	Substrate depth (cm)	Vegetation height (cm)	
Mean ± standard deviation	**185.72 ± 75.64**	**120.46 ± 61.59**	**0.68 ± 0.24**	**27.80 ± 11.21**	**12.11 ± 5.43**	**23.46 ± 10.99**	
median, IQR	**175.00, 99.00**	**110.00, 87.00**	**0.71, 0.42**	**23.70, 3.50**	**11.00, 7.00**	**21.00, 19.25**	
coefficient of variation	**40.73**	**51.13**	**35.60**	**40.35**	**44.84**	**46.86**	
Dependent variables	Plant height (cm)	Inflorescence length (cm)	Number of flowers	Number of fertilized flowers	Percentage of fertilized flowers (%)	Leaf area (cm^2)	Leaf chlorophyll concentration
Mean ± standard deviation	38.80 ± 8.45	**14.21 ± 5.18**	**25.90 ± 10.59**	**20.95 ± 10.05**	**79.70 ± 18.23**	**27.85 ± 11.02**	**28.17 ± 10.82**
median, IQR	38.50, 12.00	**15.00, 7.00**	**26.00, 13.00**	**22.00, 14.00**	**84.00, 18.00**	**26.00, 17.00**	**30.00, 14.25**
coefficient of variation	21.78	**36.42**	**40.88**	**47.99**	**22.87**	**39.56**	**38.41**

plant height on a hump index and hump slope inclination. Accordingly, the plant height on a hump index, hump slope inclination, substrate depth and vegetation height were included in the initial models.

The first two RDA axes explained 79.01% and 14.94% of the plant functional traits variation, respectively (Fig. 2). The overall model was found to be significant ($p = 0.001$), indicating that the environmental variables explained a significant portion of the variation in the plant functional traits. The RDA1 axis was highly significant ($p < 0.001$), explaining the majority of the variation in the response data. Additionally, the RDA2 axis was also significant ($p = 0.045$), although it explained a smaller portion of the variation and had a weaker effect compared to RDA1. All environmental variables were found to significantly explain variation in plant functional traits. The variables PlantH_Hump, PlantH_HumpInd, and Veg_H were all highly significant ($p = 0.001$) predictors of the response variables. The variable Hump_Inc was also significant ($p = 0.011$), although it had a smaller effect compared to the other variables.

Given the large number of dependent variables evaluated using GLMMs, Table 2 summarizes effect directions across models.

According to model selection based on AICc values (Table 3), the plant height was best explained by substrate depth and vegetation height. Plant height increased with both

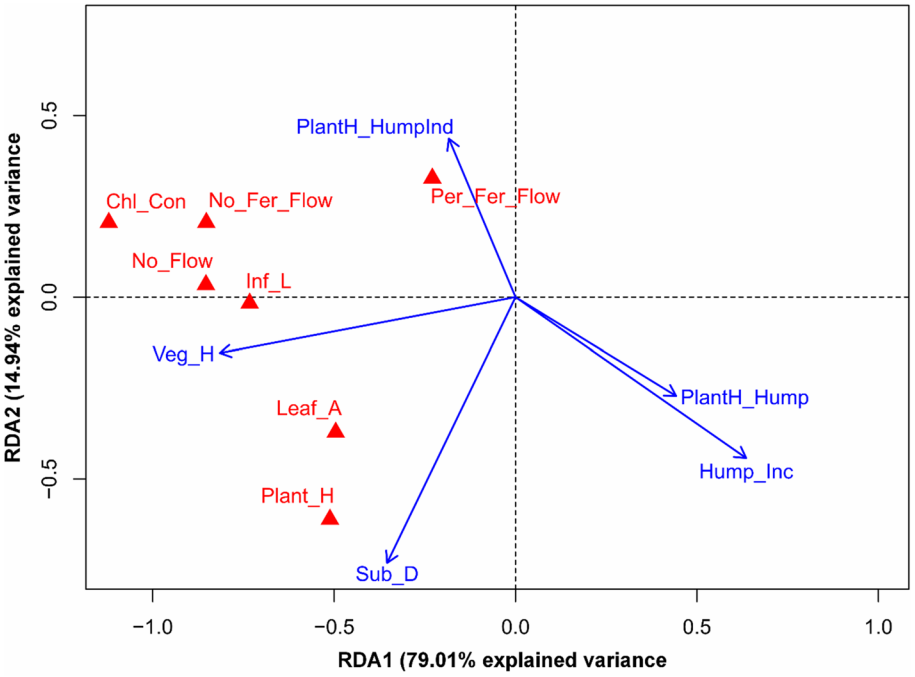


Fig. 2 RDA triplot of plant functional traits (response variables; red triangles) and environmental variables (explanatory variables; blue arrows). Arrows indicate the direction and magnitude of variables. Plant_H, plant height; Inf_L, inflorescence length; No_Flow, number of flowers; No_Fer_Flow, number of fertilized flowers; Per_Fer_Flow, percentage of fertilized flowers; Leaf_A, leaf area; Chl_Con, chlorophyll content; Hump_H, hump height; PlantH_Hump, plant height on a hump; PlantH_HumpInd, plant height on a hump index; Hump_Inc, hump slope inclination; Sub_D, substrate depth; Veg_H, vegetation (turf) height

Table 2 Summary of effect directions across GLMMs for all dependent variables. Symbols indicate the direction of effects: + positive effect, – negative effect, and/not included in the final (best) model. Full model estimates and statistical results are provided in the text

Traits↓/Predictors→	Hump height (cm)	Plant height on a hump (cm)	Plant height on a hump index	Hump slope inclination (°)	Substrate depth (cm)	Vegetation height (cm)
Plant height (cm)	/	/	/	/	+	+
Inflorescence length (cm)	/	-	+	/	+	+
Number of flowers	/	-	+	/	+	+
Number of fertilized flowers	/	-	+	/	+	+
Percentage of fertilized flowers (%)	/	-	+	/	/	/
Leaf area (cm^2)	/	/	/	/	+	+
Leaf chlorophyll concentration	/	/	/	-	/	+

Table 3 Model selection according to the corrected Akaike information criterion (AICc) and the Akaike weight (wi). Models are ordered from the most to the least appropriate. df, degrees of freedom

Model structure	df	AICc	w_i
Plant height			
$y \sim Sub_D + Veg_H + 1\|Hump$	5	2655.05	0.60
$y \sim Hump_Inc + Sub_D + Veg_H + 1\|Hump$	6	2656.85	0.24
$y \sim PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	7	2658.28	0.12
Inflorescence length			
$y \sim PlantH_Hump + PlantH_HumpInd + Sub_D + Veg_H + 1\|Hump$	7	2351.28	0.53
$y \sim PlantH_Hump + PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	8	2353.33	0.19
$y \sim PlantH_Hump + PlantH_HumpInd + Sub_D + 1\|Hump$	6	2354.27	0.12
Number of flowers			
$y \sim PlantH_Hump + PlantH_HumpInd + Sub_D + Veg_H + 1\|Hump$	7	2905.42	0.50
$y \sim PlantH_Hump + PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	8	2907.02	0.23
$y \sim PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	7	2908.54	0.11
Number of fertilized flowers			
$y \sim PlantH_Hump + PlantH_HumpInd + Sub_D + Veg_H + 1\|Hump$	7	2853.82	0.45
$y \sim PlantH_Hump + PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	8	2855.15	0.23
$y \sim PlantH_Hump + PlantH_HumpInd + Veg_H + 1\|Hump$	9	2855.67	0.18
Percentage of fertilized flowers			
$y \sim PlantH_Hump + PlantH_HumpInd + 1\|Hump$	5	3417.83	0.60
$y \sim PlantH_Hump + PlantH_HumpInd + Veg_H + 1\|Hump$	6	3419.63	0.25
$y \sim PlantH_Hump + PlantH_HumpInd + Sub_D + Veg_H + 1\|Hump$	7	3421.70	0.09
Leaf area			
$y \sim Sub_D + Veg_H + 1\|Hump$	5	2843.44	0.33
$y \sim Veg_H + 1\|Hump$	4	2843.52	0.32
$y \sim Hump_Inc + Sub_D + Veg_H + 1\|Hump$	6	2845.12	0.14
Leaf chlorophyll concentration			
$y \sim Hump_Inc + Veg_H + 1\|Hump$	5	2938.36	0.54
$y \sim Hump_Inc + Sub_D + Veg_H + 1\|Hump$	6	2940.08	0.23
$y \sim PlantH_HumpInd + Hump_Inc + Sub_D + Veg_H + 1\|Hump$	7	2941.34	0.12

substrate depth (Sub_D Estimated $\beta \pm$ SE: 0.0410 ± 0.0112, $p < 0.001$) and vegetation height (Veg_H Estimated $\beta \pm$ SE: 0.0504 ± 0.0130, $p < 0.001$) (Fig. 3a).

Plant height on a hump, plant height on a hump index, substrate depth and vegetation height best explained inflorescence length, number of flowers and number of fertilized flowers (Table 3). Inflorescence length decreased with increasing plant height on a hump (PlantH_Hump Estimated $\beta \pm$ SE: -0.0643 ± 0.0240, $p = 0.007$) and increased with plant height on a hump index (PlantH_HumpInd Estimated $\beta \pm$ SE: 0.0591 ± 0.0225, $p = 0.009$) (Fig. 3b). It was also positively associated with substrate depth (Sub_D Estimated $\beta \pm$ SE: 0.0520 ± 0.0195, $p = 0.008$) and vegetation height (Veg_H Estimated $\beta \pm$ SE: 0.0488 ± 0.0211, $p = 0.020$) (Fig. 3c). The number of flowers followed the similar trends, decreasing with increasing plant height on a hump (PlantH_Hump Estimated $\beta \pm$ SE: -0.0718 ± 0.0287, $p = 0.012$) and increasing with plant height on a hump index (PlantH_HumpInd Estimated $\beta \pm$ SE: 0.0811 ± 0.0266, $p = 0.002$) (Fig. 3d), substrate depth (Sub_D Estimated $\beta \pm$ SE: 0.0537 ± 0.0230, $p = 0.019$) and vegetation height (Veg_H Estimated

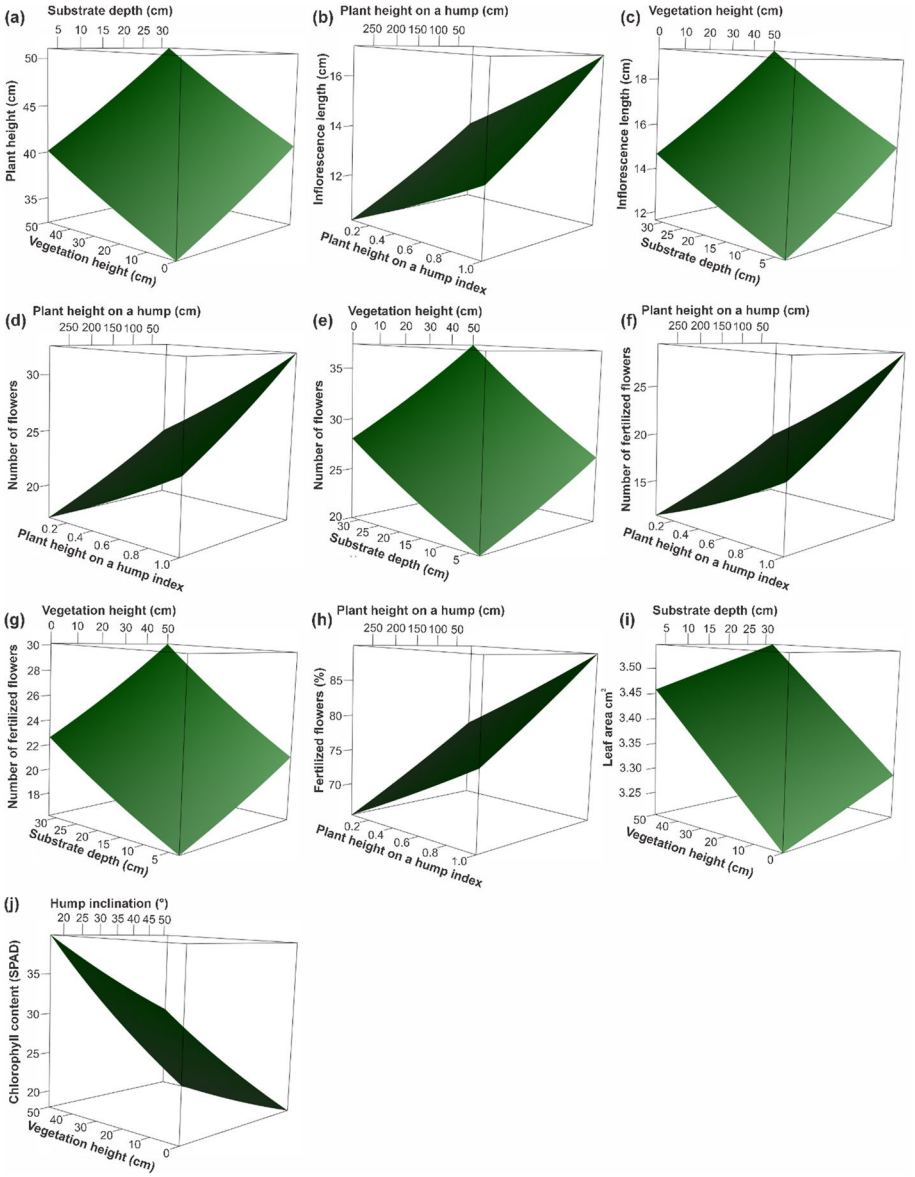


Fig. 3 Predicted values from the best GLMM models (Table 2) illustrating the effects of explanatory variables on functional traits of *N. ovata*: (**a**) – plant height**, (b, c)** – inflorescence length, (**d, e**) – number of flowers, (**f, g**) – number of fertilized flowers, (**h**) – percentage of fertilized flowers, (**i**) – leaf area, and (**j**) – chlorophyll content. In each plot, the unplotted variable is set at the mean value

β ± SE: 0.0710 ± 0.0250, $p = 0.004$) (Fig. 3e). Similarly, the number of fertilized flowers decreased with increasing plant height on a hump (PlantH_Hump Estimated β ± SE: −0.1057 ± 0.0343, $p = 0.002$) and increased with plant height on a hump index (PlantH_HumpInd Estimated β ± SE: 0.1210 ± 0.0317, $p < 0.001$) (Fig. 3f), substrate depth (Sub_D

Estimated β ± SE: 0.0538 ± 0.0273, $p = 0.048$) and vegetation height (Veg_H Estimated β ± SE: 0.0710 ± 0.0298, $p = 0.017$) (Fig. 3g).

Across all models, plant height on a hump and plant height on a hump index were key predictors of the percentage of fertilized flowers (Table 3). The percentage decreased with increasing plant height on a hump (PlantH_Hump Estimated β ± SE: −0.0362 ± 0.0183, $p = 0.048$) and increased with plant height on a hump index (PlantH_HumpInd Estimated β ± SE: 0.0385 ± 0.0174, p = 0.027) (Fig. 3h).

For total leaf area, the parameter estimates from two near-equally weighted models (Table 3) were averaged using Akaike weights, yielding the following results: leaf area increased with substrate depth (Sub_D Estimated β ± SE: 0.0326 ± 0.0222, $p = 0.144$) and vegetation height (Veg_H Estimated β ± SE: 0.0534 ± 0.0255, $p = 0.037$) (Fig. 3i).

The model including hump inclination and vegetation height best explained leaf chlorophyll concentration (Table 3). Chlorophyll concentration decreased with increasing hump inclination (Hump_I Estimated β ± SE: −0.1039 ± 0.0294, $p < 0.001$) and increased with vegetation height (Veg_H Estimated β ± SE: 0.1008 ± 0.0244, $p < 0.001$) (Fig. 3j).

Discussion

Hummocky meadow a spectrum of micro-niches

Hummocky meadows represent a specific habitat, where every hummock has slightly different biotic and abiotic properties. Hummock micro-topography establishes specific microclimatic conditions, with small-scale variations in soil thermal properties and water regimes, which influence biogeochemical cycles. These properties, coupled with different litter decomposability, may cause variations in soil physical and chemical properties and pedogenesis, as well as a selective distribution of plant species (Pintaldi et al. 2016). Many typical taxa of extensive montane grasslands with narrow ecological valence, habitat specialists prefer specific habitat conditions, specific micro sites. On the other hand, generalists are characterized by random spatial distribution within the habitat, regardless of the ecological conditions at a micro scale. However, the heterogeneity of the appropriate habitat provides a spectrum of natural gradients in the ecosystem. Generalists inhabit a wide range of ecological conditions. However, a heterogeneous habitat from a topographic perspective provides niches for generalists where they have optimal conditions as shown in this study.

Post-glacial, hummocky type of surface geomorphological profile (Embleton-Hamann 2004), has a thinner layer of soil on the hump and a thicker layer of soil in the depression (pit), with the soil layer gradually decreases towards the top of the hump. Such a profile indicates corrosion, which is explained by the fact that more water and nutrients flows into the depression, where the dissolution of the rock forms a thicker soil. The tops of the humps are dominated by washed out rendzines, while macro-elements are washed towards the pits. Pedologically, the height of the hump represents a whole spectrum of potentially favourable ecological niches. Unlike the depressions between the humps (pits), where the soil layer is usually 30 cm thick or more, the tops of the humps are the driest, and the substrate layer is thin and subject of erosion. The cross section of this profile, the hump resembles a sketch of a sinkhole. The humps vary in size, but are similar in shape. They are arranged in no particular order across former alluvial landscape. The upper convex part of the hump descends into a concave depression through the intermediate part (Lukan

Klavžer 1997). Authors agree that hummocky meadows form on unconsolidated carbonate material. Therefore, hummocky meadows are also associated with areas that are made of carbonate rocks, or were transported to this area from elsewhere, either by glacial or river transport (Cvetek 1971; Embleton-Hamann 2004). Even if considered as a habitat generalist, the specific micro-location of *N. ovata* specimens on the meadow humps plays a vital role in the plant's functional trait values and affects the spatial distribution of *N. ovata* plants.

The effect of hump and pit micro-relief on *Neottia ovata* functional traits

As shown in this study, all the environmental variables were found to significantly explain variation in plant functional traits. The variables PlantH_Hump, PlantH_HumpInd, and Veg H (Table 2) were all highly significant predictors of the response variables. According to model selection based on AICc values, the plant height was best explained by substrate depth and vegetation height. *N. ovata* plant height increases with both, substrate depth and vegetation height. Pits and lower areas of humps are characterized by deeper and more fertile substrate, creating optimal conditions for a whole spectrum of other plant species, especially grasses (fam. Poaceae). *N. ovata* plant height on a hump index, substrate depth and vegetation height best explained inflorescence length, number of flowers and number of fertilized flowers. Inflorescence length increases with increasing PlantH_HumpInd, i.e. plant height on a hump index. *N. ovata* specimens with longest inflorescences (Q1, N = 95) are found on hump slopes with mean PlantH_HumpInd value of 0.698- on micro-locations that represent 69% of the total hump height). Specimens of *N. ovata* growing higher on the humps have in general longer inflorescence compared to plants inhabiting pits or basal parts of the humps. The number of flowers followed the similar trends; increasing with plant height on a hump index, substrate depth and vegetation height. Similarly, the number of fertilized flowers increased with plant height on a hump index, substrate depth and vegetation height. Across all models, PlantH_HumpInd value was key predictor of the percentage of fertilized flowers Per_Fer_Flow. The percentage increased with plant height on a hump index. *N. ovata* specimens with highest percentage of fertilized flowers (Q1, N = 95) are found oh hump slopes with mean PlantH_HumpInd value of 0.706- on micro-locations that represent 70% of the total hump height. Proportion of the fertilized flowers goes along with plant general viability. In general reproductive success increases with plant height on a hump index. For leaf area, the parameter estimates from two near-equally weighted models were averaged using Akaike weights, yielding the following results: leaf area increased with substrate depth and vegetation height. Plants growing in pits or on the lower parts of the humps experience intense shadowing since vegetation is taller compared to hump tops. In that regard, plants respond by enlarging leaf areas in order to ensure sufficient photosynthesis. *N.* ovata specimens with the highest total leaf area values (Q1, N = 95) are found on lower parts of the humps with a mean Leaf_A value of 28.279 cm^2. In contrast, *N. ovata* specimens with the lowest total leaf area values (Q1, N = 95) are found on upper slopes and bottoms of the humps with mean Leaf_A value of 27.291 cm^2. The model including hump inclination and vegetation height best explained leaf chlorophyll concentration. Chlorophyll concentration decreased with increasing hump inclination and increased with vegetation height. In conclusion, the micro-location of *N. ovata* (expressed as plant height on a hump index values) specimens on the humps plays a vital role in plant functional trait values, it also affects plants fitness and the percentage of pollinated flowers.

Hummocky meadows, biodiverse but threatened habitat

Despite relief heterogeneity and the associated diversity of ecological niches, such meadows are degraded through leveling due to the difficulty of cultivation, mandatory manual mowing. In the winter months, when there was less agricultural activity, farmers leveled them (Cvetek 1971). Since such meadows are unsuitable for mechanical cultivation, some meadows were leveled, while others were abandoned and overgrown. However, leveling hummocky meadows is controversial, as it destroys natural, geomorphological and cultural heritage (Ambrožič 2006) in the first place. Hummocky topography significantly influences topsoil properties, pedogenesis and vegetation distribution, with large differences between hummocks and interhummocks (Pintaldi et al. 2016). A positive relationship has been reported between species richness and odds of hummock occurrence may be related to the heterogeneous microtopography created by the hummocks at those sites (Smith et al. 2012). Diversity of plant species is much greater in areas with heterogeneous microtopography (hummocked) compared to flat surfaces (Vivian-Smith 1997). In our study, we show that hummocks provide a favourable habitat for *N. ovata*. We assume there are many other species that prefer different micro habitats, which make them more or less competitive. Moreover, due to these specific properties several plant species are found only where hummocks create favourable habitat because of their heterogeneous microtopography (Smith et al. 2012). In addition, hummocky meadows are also much more diverse in terms of biodiversity than leveled meadows, as the growth conditions on humps and in depressions (pits) are very different (Prezelj 2012). Also shown in this study, ecological conditions vary greatly on the slopes of the humps. Altering them represents another threat, contributing to the homogenization of the landscapes. In addition, as shown in this study, the micro-patchiness of this particular, valuable habitat provides niches suitable for a large spectrum of different organisms. The leveling of hummocky meadows represents the loss of a diverse range of microclimatic and pedological micro-sites, which are vital for ensuring viable populations of a species, even if being considered as a habitat generalist. These, uneven grasslands in the montane belt of SE Alps represent a rich pool for further research, protecting the remaining hummocky meadows means protecting the biodiversity of the fragile alpine environment.

Research limitations

Although this study was conducted at a single site, the generalizability of the findings is not affected. The aim of the present study was to explain the micro-scale patchiness effect on the *N. ovata* functional traits, and not comparing differences in ecological values among humps across multiple meadows, sites.

Acknowledgements The authors sincerely thank the three anonymous reviewers for their insightful comments, which contributed to the improvement of the manuscript. Peter Kozel acknowledges the Karst Research programme (research core Funding no. P6-0119). This work was partly supported by the project "Development of Research Infrastructure for the International Competitiveness of the Slovenian RRI Space – RI-SI-LifeWatch", co-financed by the Republic of Slovenia, Ministry of Education, Science and Sport and the European Union from the European Regional Development Fund and EU Research Infrastructure eLTER ERIC and LifeWatch ERIC.

Author contribution I.P began the research, led the research and wrote most of the article, T.G. assisted with fieldwork and editing the article, K.P. did the field work, P.K. performed statistical analyses and edited the article.

Data availability The data that support the findings of this study are available from the authors upon reasonable request.

Declarations

Competing interests The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Ambrožič T. 2006. Hummocky meadows in Zgornja Radovna. Graduation thesis, University of Ljubljana, Biotechnical Faculty, Department of Agronomy, 94 pp.

Bartoń, K. 2025. MuMIn: Multi-Model Inference. R package version 1.48.4. https://CRAN.R-project.org/package=MuMIn

Bell G. Spatial heterogeneity at small scales and how plants respond to it. Exploitation of environmental heterogeneity by plants. 1994:391-414. https://doi.org/10.1016/b978-0-12-155070-7.50019-6.

Bolker BM (2003) Combining endogenous and exogenous spatial variability in analytical population models. Theor Popul Biol 64(3):255–270. https://doi.org/10.1016/s0040-5809(03)00090-x

Brooks, M., Bolker, B., Kristensen, K. Maechler, M., Magnusson, A., McGillycuddy, M., Skaug, H., Nielsen, A., Berg C., van Bentham, K., Sadat, N., Lüdecke, D., Lenth, R., O'Brien, J., Geyer, C.J., Jagan, M., Wiernik, B., Stouffer, D.B., Agronah, M. 2024. glmmTMB: Generalized Linear Mixed Models using Template Model Builder. R package version 1.1.10. https://CRAN.R-project.org/package=glmmTMB

Brzosko E, Bajguz A, Chmur M, Burzyńska J, Jermakowicz E, Mirski P, Zieliński P (2021) How are the flower structure and nectar composition of the generalistic orchid *Neottia ovata* adapted to a wide range of pollinators? Int J Mol Sci 22(4):2214. https://doi.org/10.3390/ijms22042214

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, NY

Costanza JK, Moody A, Peet RK (2011) Multi-scale environmental heterogeneity as a predictor of plant species richness. Landscape Ecol 26(6):851–864. https://doi.org/10.1007/s10980-011-9613-3

Cvetek J (1971) Grbinasti travniki s posebnim ozirom na Bohinj. Geogr Vestn 42:67–78

Davies KW, Bates JD, Miller RF (2007) Environmental and vegetation relationships of the *Artemisia tridentata* spp. *wyomingensis* alliance. J Arid Environ 70(3):478–494. https://doi.org/10.1016/j.jaridenv.2007.01.010

Delforge P (2006) Orchids of Europe, North Africa and the Middle East. Christopher Helm Publishers, Incorporated

Dylikowa A (1956) Formes contemporaines du type congélifluctif sur le Turbacz (Gorce – Carpates). Biul Peryglac 4:339–344

Embleton-Hamann C (2004) Processes responsible for the development of a pit and mound microrelief. CATENA 57(2):175–188. https://doi.org/10.1016/j.catena.2003.10.017

Gerlach T (1960) Report on the origin of small earth hillocks on the Hala Długa in the Gorce range. Prz Geol 32:86–93

Hara M, Hirata K, Fujihara M, Oono K (1996) Vegetation structure in relation to micro-landform in an evergreen broad-leaved forest on Amami Ohshima Island, south-west Japan. Ecol Res 11(3):325–337. https://doi.org/10.1007/bf02347790

Hastie, T. 2023. gam: Generalized Additive Models. R package version 1.22–2. https://CRAN.R-project.org/package=gam
Kephart SR, Paladino C (1997) Demographic change and microhabitat variability in a grassland endemic, *Silene douglasii* var. *oraria* (Caryophyllaceae). Am J Bot 84(2):179–189. https://doi.org/10.2307/2446079
Kotilínek M, Tatarenko IV, Jersáková J (2015) Biological flora of the British Isles:*Neottia ovata*. J Ecol 103(5):1354–1366. https://doi.org/10.1111/1365-2745.12444
Lukan Klavžer T (1997) Grbinasti travniki. Gea 7(1):54–55
Macarthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, N.J
Murdoch D, Adler D 2023. rgl: 3D Visualization Using OpenGL. R package version 1.0.1. https://CRAN.R-project.org/package=rgl
Oksanen, F.J., et al. 2025. Vegan: Community Ecology Package. R package Version 2.6–10. https://mirror.ibcp.fr/pub/CRAN/web/packages/vegan/vegan.pdf
Olagoke A, Jeltsch F, Tietjen B, Berger U, Ritter H, Maaß S (2023) Small-scale heterogeneity shapes grassland diversity in low-to-intermediate resource environments. J Vegetat Sci 34(4):e13196. https://doi.org/10.1111/jvs.13196
Palmer MW, Dixon PM (1990) Small-scale environmental heterogeneity and the analysis of species distributions along gradients. J Veg Sci 1(1):57–65. https://doi.org/10.2307/3236053
Pintaldi E, D'Amico ME, Siniscalco C, Cremonese E, Celi L, Filippa G, Prati M, Freppaz M (2016) Hummocks affect soil properties and soil-vegetation relationships in a subalpine grassland (North-Western Italian Alps). CATENA 145:214–226. https://doi.org/10.1016/j.catena.2016.06.014
Preston CD, Hill MO (1997) The geographical relationships of British and Irish vascular plants. Bot J Linn Soc 124(1):1–120. https://doi.org/10.1111/j.1095-8339.1997.tb01785.x
Prezelj K. 2012. Vegetation and humidity conditions on the hummocky meadows in Zgornja Radovna and Krma areas. Graduation thesis, University of Ljubljana, Biotechnical Faculty, Department of Agronomy, 67 pp.
R Core Team. 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Ricklefs RE (1977) Environmental heterogeneity and plant species diversity: a hypothesis. Am Nat 111(978):376–381. https://doi.org/10.1086/283169
Smith ML, Meiman PJ, Brummer JE (2012) Characteristics of hummocked and non-hummocked Colorado riparian areas and wetlands. Wetl Ecol Manage 20(5):409–418. https://doi.org/10.1007/s11273-012-9263-5
Swenson NG, Anglada-Cordero P, Barone JA (2010) Deterministic tropical tree community turnover: evidence from patterns of functional beta diversity along an elevational gradient. Proceed Royal Soc: Biologic Sci 278(1707):877–884. https://doi.org/10.1098/rspb.2010.1369
Tałałaj I, Ostrowiecka B, Włostowska E, Rutkowska A, Brzosko E (2017) The ability of spontaneous autogamy in four orchid species: *Cephalanthera rubra*, *Neottia ovata*, *Gymnadenia conopsea*, and *Platanthera bifolia*. Acta Biol Cracov Ser Bot 59(2):51–61. https://doi.org/10.1515/abcsb-2017-0006
Tamm C.O. 1991. Behavior of some orchid populations in a changing enviroment - observation on permanent plots, 1943–1990. Population Ecology of Terrestrial Orchids (eds T.C.E. Wells & J.H. Willems), pp. 1–13. SPB Academic Publishing, The Hague, the Netherlands.
Vivian-Smith G (1997) Microtopographic heterogeneity and floristic diversity in experimental wetland communities. J Ecol 85(1):71. https://doi.org/10.2307/2960628
Zhang Q, Wang J, Wang Q (2021) Effects of abiotic factors on plant diversity and species distribution of alpine meadow plants. Ecol Informatics 61:101210. https://doi.org/10.1016/j.ecoinf.2021.101210
Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. Methods Ecol Evol 7(6):636–645. https://doi.org/10.1111/2041-210x.12577. (Freckleton R, editor)
Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer New York, New York, NY
Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1(1):3–14. https://doi.org/10.1111/j.2041-210x.2009.00001.x
Zuur AF, Hilbe JM, Ieno EN (2013) A beginner's guide to GLM and GLMM with R. Highland Statistics Ltd., Newburgh

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.